Structure and pattern of native and alien plant communities across local and global scales

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Declaration

Plant species data used in part of Chapter 2, Chapter 3 and Chapter 4 was collected by Hugh Wilson. Permission to use these data was given by Hugh Wilson to myself. The data references are provided in Chapter 2. Chapter 5 uses a database which contains relevant articles that I personally collected from several sources.

Some of the thesis material was also presented in Italian on the TV program "Talenti d'Italia" broadcast in Italy on the national Rai Due tv channel on 11th December 2012.

The following manuscript forming Chapter 4 has been published and it is freely available online as:

Tomasetto, F., Duncan, R. P. & Hulme, P. E. (2013) Environmental gradients shift the direction of the relationship between native and alien plant species richness. *Diversity and Distributions*, 19:49-59. See Appendix K.

The world is not inherited from our fathers
but borrowed from our children

Abstract

Identifying and quantifying the abiotic and biotic factors that influence the structure and pattern of native and alien plant species communities is of crucial importance in invasion ecology. There is little knowledge of how these factors covary with dominant environmental gradients and affect the plant communities especially in heavily modified landscape.

In my thesis, I focus on how these factors covary with dominant environmental gradients and influence the composition and structure and richness patterns of native and alien plant communities on Banks Peninsula (New Zealand). The invasion of alien plant species frequently shows an alteration in the native community composition and structure (e.g. increasing biotic homogenization). The native-alien species richness relationship (NARR) is used here as an ecological indicator for assessing community invasibility. Factors underlying NARR are crucial for understanding community assembly and are here investigated across local scale (i.e. species communities), regional-landscape scale (i.e. Banks Peninsula) and global scale.

Using Banks Peninsula as a model system, I tested the relative importance of factors that drive the invasion process on the Peninsula and set this within a global context, using GIS, multivariate statistical techniques and spatial regressions to analyse how these factors interact with native and alien plant communities to determine composition and structure and richness patterns. The species richness relationship at local and regional-landscape scales is contextualised on a global scale using a meta-analytical approach to the considerable body of literature on NARR and so to clarify the so-called "invasion paradox", which has not been adequately quantified so far.

Across a heterogeneous environment such as Banks Peninsula, native and alien species communities were found to be spatially and ecologically segregated according to different responses, firstly, to land-use and -management and, secondly, to climate and environmental factors, both of which covary with elevational gradients. Both

positive and negative relationships between native and alien species richness can arise, with this outcome moderated by the effects of land-use history and management. Globally, a significant positive NARR was found with plot size consistently the best predictor. For studies sub-grouped by plot size, NARR increased positively and significantly with increasing plot size.

Across Banks Peninsula, high levels of human-related disturbance offer the best conditions for the spread of alien species and for an increased homogenization effect of the native community. In areas characterized by high intensity levels of land-management, biotic homogenization is stronger and a more serious problem than in less managed areas. Across Banks Peninsula, negative NARR can be attributed, not to biotic resistance, but mainly to the shift in community types as a consequence of land-use history and management along elevational gradients. Globally, NARR is overall positive and scale dependent. However, negative and positive NARR can occur within the same plot size and across the same landscape, depending on the plant community and the underlying gradients examined.

It is therefore important to take into account human-related factors or proxy measures (e.g. land-use history and management) when studying drivers of plant invasions, because these are the primary factors in explaining composition and structure and richness patterns of native and alien species communities at local and regional-landscape scale.

Keywords: Biological invasions, biotic interactions, biotic homogenization, climate, data exploration, dissimilarity, disturbance, effect size, elevational gradient, exotic species, GIS, habitat heterogeneity, land-use change, meta-regression, nestedness, plant invasion, Remote Sensing, sampling design, scale-dependence, weeds

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Abbreviations

Abbreviation	Definition
AIC	Akaike Information Criterion
GIS	Geographic Information Systems
GLS	Generalized Least Squares
LINZ	Land Information New Zealand
MANOVA	Multivariate Analysis of Variance
NARR	Native-Alien Richness Relationship
NIWA	National Institute of Water and Atmospheric Research
NMDS	Non-Metric Multidimensional Scaling technique
NODF	Nestedness metric based on Overlap and Decreasing Fill
NZLRI	New Zealand Land Resource Inventory
NZ REC	New Zealand River Environment Classification
OFD	Occupancy Frequency Distribution
RS	Remote Sensing
RMSE	Root Mean-Squared Error
ROR	Rank Occupancy Rate
VBA	Visual Basic for Application
VIF	Variance Inflation Factors

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Chapter 1

Introduction

1.1 The problem of plant invasions

The invasion of alien plant species is an important global change issue. It is widely accepted that the invasion of alien plants involves serious ecological losses (Hobbs and Humphries, 1995; Dukes and Mooney, 1999; Pimentel *et al.*, 2011) with resulting challenges for the conservation of biodiversity and natural resource. The invasion of alien plant species, in fact, frequently shows an alteration in the composition and diversity of the native species communities (Vitousek *et al.*, 1997), increasing, for example, local extinction rates and promoting biological homogenization (Wiser *et al.*, 1998; Hulme, 2003; McKinney, 2006; Pyšek and Richardson, 2006; Lambdon *et al.*, 2008; Winter *et al.*, 2009) or altering the species community structure, for example, leading to nested distributions where the alien species might be more nested than native species (Foxcroft *et al.*, 2007; Vilá *et al.*, 2009a; Baeten *et al.*, 2012) or altering the structure and functioning of whole ecosystems (Pyšek and Richardson, 2010).

Plant invasions also impose economic costs (Simberloff *et al.*, 2013). Pimentel *et al.* (2005) estimated that the economic impact of invasive alien plant species in the USA was $34 billion per year. An attempt at quantifying the economic cost of naturalized plant species which had become invasive to New Zealand (i.e. weeds; *sensu* Pyšek *et al.*, 2004) was undertaken by Williams and Timmins (2011). They categorised the costs in 2008 as defensive expenditure, which is the financial cost of resources devoted to preventing pest plants from entering the country and managing the populations of those already here, and as the loss of economic output, and found that the amount spent to protect the country against weeds came to *c.* $130 million per year. Bourdot *et al.* (2007) determined that 187 pastoral weeds, classified as perennial or annual grasses and forbs, shrubs, trees, and plants with bulbs or tubers, are present in the nearly 12 million ha of agricultural land grazed by livestock in New Zealand. Weeds represent a threat not only to natural habitats but also to managed ecosystems (Pimentel *et al.*, 2011) and have economic consequences for human activities reducing pastoral output and adding significant costs to production, as has been found in the United States (Duncan *et al.*, 2009), in China (Brock and Wu, 2008) and in New Zealand (Williams and Timmins, 2011). The current aggregate cost of pastoral weed species to the New Zealand economy is estimated to be NZ $1.2 billion per annum based on an analysis made in 1984 (Anonymous, 1984). However, this analysis needs to be treated with considerable caution because of a

lack of both objective data on the impact of weeds on pastoral production and the lack of accurate and comprehensive national census of the main problem species.

1.2 The invasion history of New Zealand

Alien species have undoubtedly invaded New Zealand in a way that is not comparable elsewhere in the world (Lee *et al.*, 2006). New Zealand, a historically isolated and ancient landmass, has in fact suffered severe damage from invasive species, especially by temperate grassland species from Europe and North America (Fenner and Lee, 2001). A comparison with Australia, a continental area 29 times larger than New Zealand, gives an idea of the current level of invasion. In New Zealand *c.* 28000 alien species have been intentionally or unintentionally introduced since 1840 (Williams and Cameron, 2006), with the same number being found in Australia (Diez *et al.*, 2009b). However, in proportion to the unit area and the total flora, New Zealand has more naturalized plant species than Australia (Diez *et al.*, 2009b). Today, it is placed among the most highly invaded areas on earth (Pimentel *et al.*, 2011; Williams and Timmins, 2011) with naturalized alien seed plant species outnumber native species (Williams and West, 2000; Wilton and Breitwieser, 2000; Popay *et al.*, 2002; Williams and Newfield, 2002; Williams and Timmins, 2011).

Introductions of alien species into New Zealand are obviously dependent on human-assisted transportation (Lee *et al.*, 2006). Introduced plants (but also animals) intentionally enter the country in sufficient quantity for commercial reasons (Lee *et al.*, 2006). Not only in New Zealand but also elsewhere, it is recognised that species for gardening and urban landscaping often become invasive (Hulme, 2007; Niinemets and Peñuelas, 2008) and human-related activities disperse propagules over large areas where suitable sites for establishment might be more likely to be found (Wilson *et al.*, 2009; Hoffmann, 2010). In New Zealand, regional human population densities and the number of people in the region are also positively related to the number of naturalized plant species (Allan, 1937; Webb *et al.*, 1988; Sullivan *et al.*, 2004; Williams and Cameron, 2006). This is also verified in the rangelands in USA (Lonsdale and Milton, 2002) and across Europe (Pyšek *et al.*, 2010b). In addition, proximity to settlements, human use, presence of rubbish and distance from road or railway line are the most important predictors of the number of environmental weeds in New Zealand lowland forest reserves and coastal forest fragments (Timmins and Williams, 1991; Sullivan *et al.*, 2005) because there is a

high frequency of human visits to reserves, dumping of garden waste and foraging of birds that disperse seeds of alien plants. Moreover, Aikio *et al.* (2012) found out that forest and grassland contain similar number of alien species and roadside and lakeshore that are respectively the most and the least invaded habitats in New Zealand.

Habitat modification, as a consequence of disturbance, is an additional important factor in the invasion process. According to Craine *et al.* (2006), New Zealand habitats can be considered a collection of niches: (1) novel (i.e. most recent in origin, less broad in space and more discontinuous in space or time) and, (2) core niches (i.e. with wider spatio-temporal extent and/or continuity through time). With the occurrence of natural and human-related disturbance, novel niches have been created and these niches might be more prone to be invaded by alien plant species (Craine *et al.*, 2006). It is in fact widely accepted that disturbance promotes invasion (Crawley, 1987; Hobbs, 1989; Mack and D'Antonio, 1998; Godfree *et al.*, 2004).

The major and historical disturbances for the New Zealand's flora that influence the composition and structure and richness patterns of plant communities are frequent fires or large mammalian herbivores (Mark, 1965; Buchanan, 1968; Scott *et al.*, 1988; Calder *et al.*, 1992; Yeates and Lee, 1997; Mark and Dickinson, 2003; Ewans, 2004; Espie and Barratt, 2006). Naturally, changes in ecosystems composition and structure and functioning due to fire cycle occur elsewhere, both in continental and in insular systems (D'Antonio and Vitousek, 1992; Brooks *et al.*, 2004; Bradley and Mustard, 2006). These disturbances can be seen as consumers of vegetation affecting the native flora that evolved in the absence of both fire and herbivores (Bond and Keeley, 2005). Especially in tussock grasslands, the introduction of both of these factors during Polynesian (Maori) and European settlement periods had dramatic impacts on plant community composition and structure (Mark, 1965; Calder *et al.*, 1992; Mark, 1994; Rose *et al.*, 1995; Yeates and Lee, 1997; Walker and Lee, 2000; Duncan *et al.*, 2001; Day and Buckley, 2011). Burning frequency, in fact, increased during European settlement to maintain grasslands for grazing, primarily by sheep (*Ovis* spp.; Buchanan, 1968; Mark and Dickinson, 2003). Burning is still used as a land-use management tool to enhance growth of palatable species and clear areas for oversowing of alien pasture species, but with less frequency nowadays (Scott *et al.*, 1988; Espie and Barratt, 2006).

The burning and loss of native forest were strongly associated with Polynesian, first, and European settlers after (Williams and West, 2000; McWethy *et al.*, 2009). More than 60% of all New Zealand's indigenous habitats have been, in fact, converted

for agriculture and forestry (McGlone, 2001). These human-related activities had consequences for the whole plant community, ultimately leading to invasion by alien species (Wilson and Meurk, 2011). Although in New Zealand, native forests have historically been considered widely resistant to invasion (Wiser and Allen, 2006), alien plant invasion is occurring. This is not controlled by disturbance, substrate and soil fertility (Wiser *et al.*, 1998) but instead by species richness (Wiser and Allen, 2006). In general, species richness has a positive effect on invasion. Possible explanations include: increased temporal and spatial heterogeneity of abiotic and biotic conditions within species-rich sites (Wiser *et al.*, 1998); or the positive effects of arbuscular mycorrhizas (Wiser and Allen, 2006).

So, what kind of plant communities in New Zealand shows high levels of plant invasion? The interactions of human-related disturbance (e.g. fire, grazing and agriculture) together with propagule pressure are likely to homogenize the composition of the flora (Mack, 1989). In particular, temperate grasslands are well suited for growing several crop species and pasture and these are among the most susceptible communities to invasion (Mack, 1989). According to Mack (1989), grasslands in countries that were recently colonized (e.g. North, South and West America, Australia and New Zealand) are predestined to be devastated by plant invasions. In New Zealand and only after 1970s, the spread and impacts of several alien plant species became too obvious to be ignored (Lee *et al.*, 2006). Specifically, the continental climates in New Zealand have been probably the areas most affected by invasion of alien plant species (Craine *et al.*, 2006). In addition, a wide range of annual, biennial and perennial plant species, grasses and forbs from California and the Mediterranean areas have invaded low-rainfall areas over the last 150 years (Walker and Lee, 2000; Craine *et al.*, 2006).

In this context, tussock grasslands are one of the most modified and invaded habitats in New Zealand (Mark, 1994; Duncan *et al.*, 2001; Day and Buckley, 2011). From late 1800s when Europeans arrived, they started land-use activities, such as pastoral farming, introducing palatable alien plant species to tussock grasslands to increase domestic stock, mainly for sheep and cattle, and to prevent soil erosion due to overgrazing (O'Connor, 2003). The alien species that Europeans introduced into New Zealand were either pre-selected for their facility to grow in pastures that were fertilized and/or they were grown together in sward with *Trifolium* spp. (Craine *et al.*, 2006). In New Zealand, native species provided little in this respect. In fact, New Zealand native grasslands tend to occupy cold, wet sites, and they also have traits associated with low nutrient supply whereas introduced species have traits

associated with high nutrient supply (Craine and Lee, 2003; Craine *et al.*, 2006; Gross *et al.*, 2013). In addition, New Zealand flora has high level of endemicity that is predominantly perennial and slow-growing (Meurk *et al.*, 1989; Wardle, 1991).

As consequence, the fast-growing alien plant species can outcompete these slower-growing native species and this has led to competitive exclusion and declines in native species in localised areas (Lord, 1990; Rose *et al.*, 1998; Walker and Lee, 2000; Walker *et al.*, 2003). For instance, studies of vegetation change over the last four decades in the high country tussock grasslands of the South Island in New Zealand have undergone major changes in composition and structure and richness patterns of native and alien plant communities, generally towards increased dominance by alien species and reductions in the richness and abundance of native species (Scott *et al.*, 1988; Treskonova, 1991; Rose *et al.*, 1995; Johnstone *et al.*, 1999; Duncan *et al.*, 2001; Day and Buckley, 2011). Alien grass and herb species were sown on land cleared from forest and fern (Cockayne, 1919; O'Connor, 1982; Duncan *et al.*, 2001; Day and Buckley, 2011). Annual and biennial life-forms are well represented among alien plant species, together with wind-dispersed perennials that effectively colonize disturbed areas (Craine *et al.*, 2006). *Agrostis capillaris*, *Rytidosperma* spp., *Anthoxanthum odoratum*, *Trifolium dubium*, *Lolium perenne*, *Poa pratensis* and several clover species were the most sown herbaceous species (Williams and Cameron, 2006; Meurk, 2008).

Another relevant factor that may drive the level of invasions can be found in the high or low grazing levels. Several mammalian herbivores are now widespread on the mainland, with most of the native grassland communities being grazed mainly by the domestic sheep (*Ovis aries*) from the valley floors to alpine regions (Burrows and Wilson, 2008). Alien species are more adapted to grazing and browsing disturbance, due to different traits such as chemical defences (e.g. *Hieracium* and *Anthoxanthum*) or physical defences (e.g. *Ulex europeaus*) or having a grazing-tolerant growth form (e.g. *Agrostis*) (Craine *et al.*, 2006). Not only grazing but also human-related disturbances that are associated with settlement and agriculture maintain open ground that facilitates the spread and colonization of alien species (Craine *et al.*, 2006). In this ecological context, alien species are increasingly displacing native species in grassland communities. In particular, areas that are grazed by sheep and cattle frequently contain dominant alien grass species (Lee *et al.*, 2006).

One well documented example can be found in the impact of European pastoralism on the native grasslands of the eastern South Island (O'Connor, 1982; Mark, 1994). Continued grazing activities mainly by sheep and cattle in tussock grasslands

resulted in a marked decline of native species richness, such as *Chionochloa* spp., and an increase of the abundance of aliens, such as *Hieracium* spp. [Treskonova (1991); c.f. Scott *et al.* (1988); Rose *et al.* (1995)]. Currently, few areas of native grassland remain without some degree of modification [Ewans (2004) and citations therein].

What are the consequences for New Zealand grassland if areas are closed to grazing? An example can be found in a study by Rose *et al.* (1995), where the authors examined different grazing histories (continually grazed versus ungrazed) in short tussock grassland between 700 m and 1350 m a.s.l.. In general, there was a trend towards invasion by alien species such as *Agrostis capillaris* and *Hieracium* spp. and a decline in native grassland species such as short tussock grasses (e.g. *Festuca* spp. and *Poa* spp.). However, the effects of grazing history varied along aspect and elevation. Another example is given by Ewans (2004). The author highlighted how the extent of floristic changes is greater at wetter sites and/or at the sites with the longer period since the enclosure to grazing. He suggested that if we remove grazing this results in an increase in the cover of naturalized plants, especially grass species, and a decrease in the number and/or cover of native herbaceous species (Ewans, 2004). Several studies have also found that alien grass species, such as *Agrostis capillaris* and *Anthoxanthum odoratum*, increase in tussock grasslands after grazing cessation because these alien species are successful at colonising novel niches and disturbed habitats (Rose *et al.*, 1995, 1998; Grove *et al.*, 2002; Espie and Barratt, 2006) while alien plant species such as *Hieracium* spp. increased locally even with or without grazing (Rose and Frampton, 2007).

Consequently, there is uncertainty about the extent to which recent changes in tussock grassland have been driven primarily by land-use history and management (i.e. historical or recent pastoral activities) or whether other processes are more important in driving vegetation change (Duncan *et al.*, 2001). Teasing apart these drivers is an important part of invasion ecology and is the focus of my particular work on Banks Peninsula.

Is there any native grassland that remains without some degree of disturbance? What about the variation in the level of invasion in New Zealand grasslands with altitude? In many mountain grasslands, grazing is still present and has major consequences. Craine *et al.* (2006) found that grazing by sheep rapidly consumed native plant species and deteriorated montane grasslands. Grasslands comprised of native species such as *Chionochloa* spp., *Festuca* spp. and *Poa* spp. are, in fact, poorly adapted to foraging by grazing mammals. Duncan *et al.* (2001) highlighted that since European arrival and the start of pastoral farming in the late 1800s, particularly the

introduction of sheep, cattle and feral rabbits, and the increase in burning frequency associated with stock grazing, the high country tussock grasslands of the South Island, New Zealand, have also undergone major changes in vegetation composition and structure. One of the most dramatic results was the widespread development of tussock grasslands with the replacement of tall tussock (*Chionochloa* spp.) grassland with short tussock (*Festuca novae-zelandiae*) grassland and consequently a shift towards low-growing alien species dominated communities (Cockayne, 1919; Zotov, 1947; Connor and Vucetich, 1964; Connor, 1965; O'Connor, 1982; Burrows and Wilson, 2008; Meurk, 2008). Other studies in grasslands in Fiordland between 900 and 1600 m a.s.l. (Rose *et al.*, 1998), in Central Otago below 460 m a.s.l. (Wilson *et al.*, 1989) and in the Harper-Avoca Valley between 700 and 1350 m a.s.l. (Rose *et al.*, 1995) found that native and alien species composition along with the proportion of alien in the flora reflected an elevational gradient. Wilson (1989) found that in semi-natural to high managed pasture areas of the South Island in New Zealand, native and alien species communities composition differed spatially and ecologically and these were differently related to environmental factors (e.g. elevation, soil fertility and water) as other studies have found in other modified landscapes worldwide (Oneal and Rotenberry, 2008; Brown and Boutin, 2009; Otýpková *et al.*, 2011). A study of plant species composition and structure in the Canterbury Plains in the South Island in New Zealand conducted by Meurk (2008) identified 9 vegetation types that reflect the relationships between plants species and environmental gradients (mainly different soil conditions). Similar to other case studies (Wilson, 1989; Wiser and Buxton, 2009), Meurk (2008) found that native and alien plant species segregate differently along environmental gradients resulting in different spatial and ecological patterns, with degraded native vegetation opposed to broadly extended alien species communities.

My related study therefore seeks to determine how abiotic and biotic drivers co-vary with dominant environmental gradients (i.e. land-use history and management and climate-environmental factors) and influence native and alien species composition and structure and richness patterns in the Ecological Region of Banks Peninsula (New Zealand). This thesis will also attempt to identify which plant communities are already invaded and/or more likely to be invaded. As Fridley (2011) has pointed out, understanding the drivers underlying plant invasions is important "for conservation efforts that seek to prioritize areas for invasive species control and prevention, for ecological restoration efforts that seek to create invasion resistant communities, and

for understanding the processes that govern community assembly across a variety of ecosystems".

1.3 Banks Peninsula (New Zealand) as a model system

The Banks Peninsula (*c.* 1000 km^2) on the south-east coast of the South Island, New Zealand, is an example of an area in which a wide range of native and alien plant species and animals coexist within a landscape of both natural and managed status. The highly varied topography (e.g. altitude ranges from 0 to 920 m a.s.l.) is characterized by soils that are typically well drained and of moderate to high fertility (Speight, 1943; Williams, 1983; Sewell *et al.*, 1992; Wilson, 2009), with annual rainfall ranges from 600 mm at the driest low elevation sites to 2000 mm at higher elevations and a mean daily temperature ranges from 8 to 13°C.

The need to establish a system of reserves that would cover the country's ecological diversity led to the concept of dividing New Zealand into Ecological Regions (McEwen, 1987). One of the 85 regions is the Banks Peninsula. This is a rich Ecological Region containing remnant original forest, regenerating native shrub and forest, tussocks, and productive farmland (Wilson, 2009). Several native plant species reach their southern or northern limits here. In its mosaic of habitats live threatened plant species and animals, as well as six endemic plant species. Much of the ancient forests of podocarp/hardwood forest present in pre-human times have been lost after changes in the landscape as a result of the impact of Maori and European settlement, as in other areas of New Zealand (McEwen, 1987; Rose *et al.*, 1998; Williams and West, 2000; Duncan *et al.*, 2001; McWethy *et al.*, 2009; Wilson and Meurk, 2011).

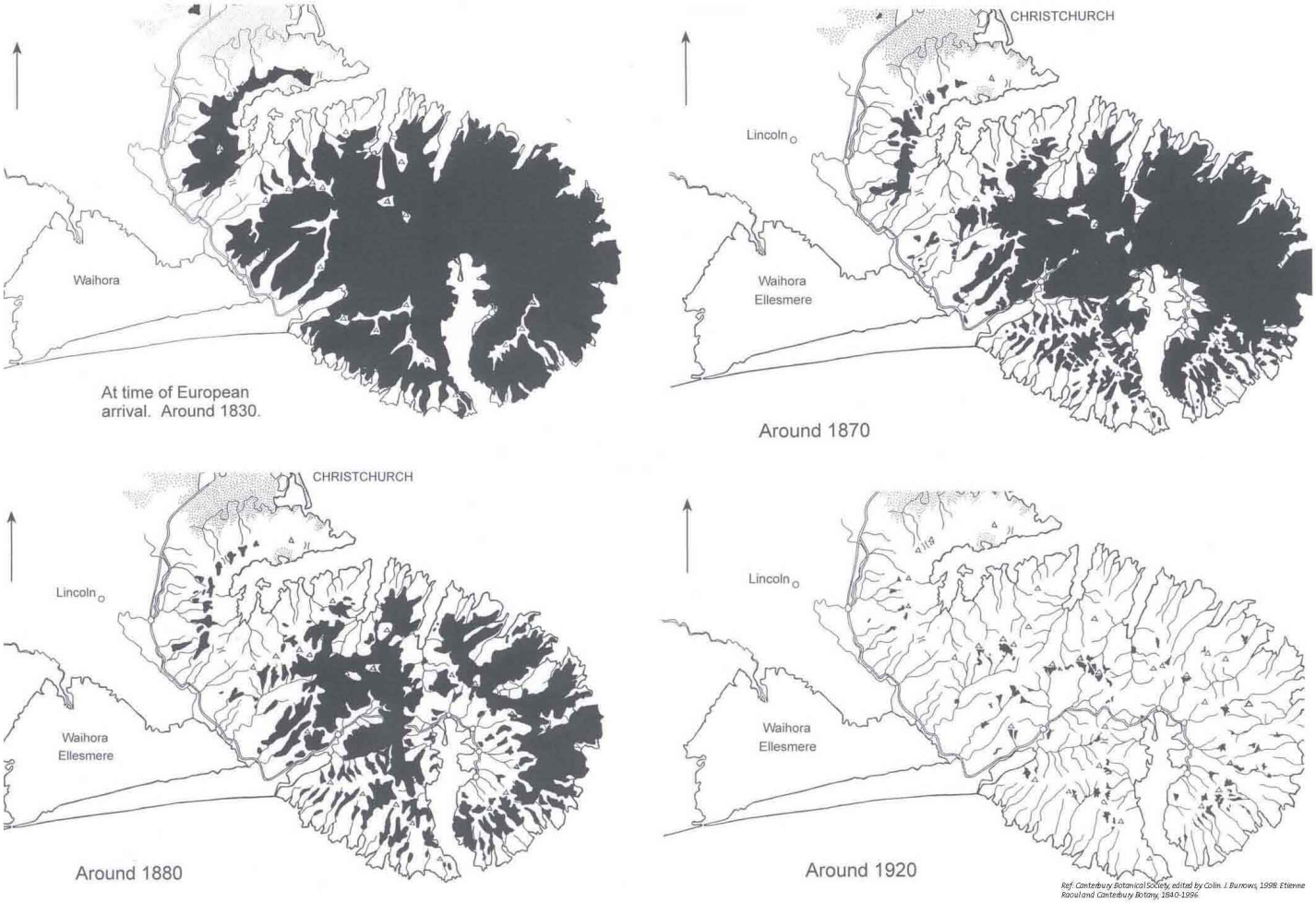

Figure 1.1. Native Forest Cover changes of Banks Peninsula since 1830 reprinted from Wilson (1998).

In the mid-1800s forest was extensively cleared and converted to grassland for farming, such that by 1920 less than 1% of the original forest cover remained (Figure 1.1; Wilson, 1998; Schmechel, 2005; Wilson, 2008, 2009). In less intensively farmed areas, typically at higher elevation and in less-accessible locations, forest clearance and burning has led to forest replacement by grassland dominated by native tussocks. On more accessible and productive, typically low- to mid-elevation, sites more intensive burning, oversowing with pasture species, fertiliser addition and livestock grazing led to the removal of native tussocks and their replacement by grasslands dominated almost entirely by improved alien pasture species. These areas converted for agriculture, farming and forestry are a typical feature of the natural history of the South Island (Weeks *et al.*, 2013) where, as a consequence of human-related disturbances, native tussock grasslands are under threat (Rose *et al.*, 1998; Ewers *et al.*, 2006) and these communities may show high levels of plant invasion. Several New Zealand studies have in fact demonstrated that levels of invasion may be directly affected by disturbance from fire and/or grazing (Rose *et al.*, 1995; Meurk *et al.*, 2002; Bellingham and Coomes, 2003).

In this context of human-driven conditions, Banks Peninsula now supports a large number of introduced species mostly of European origins (Figure 1.2). These species are now naturalized or cultivated and found in road verges, farmland, plantations, and residential areas. Nowadays, 285 species classified as fully naturalized (*sensu* Pyšek *et al.*, 2004) are found on the Peninsula. A high number of introduced species that probably outnumber the native flora, but mainly in cultivated areas, is also found on the Canterbury Plains, the land that connect the Banks Peninsula to the Southern Alps of New Zealand (Meurk, 2008).

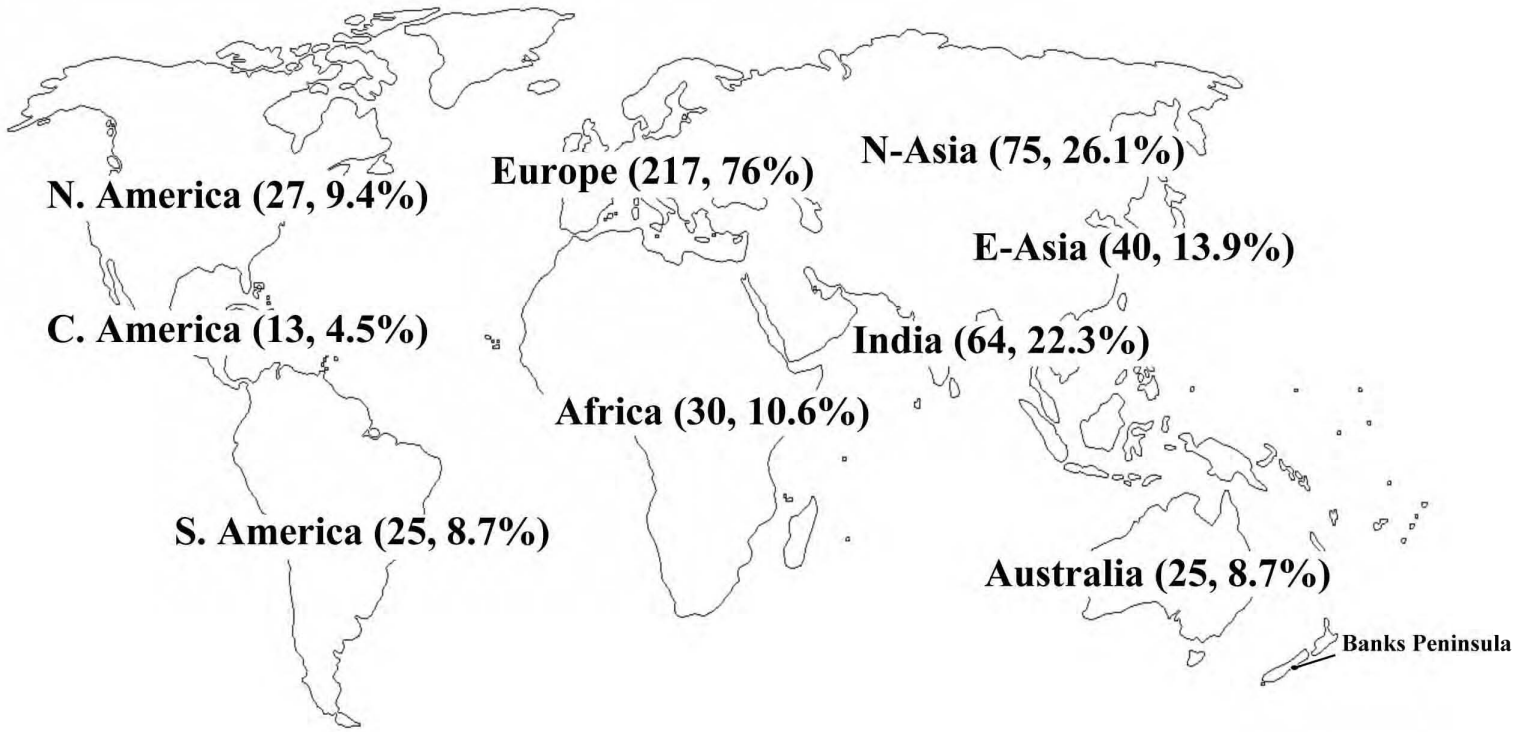

Figure 1.2. Origins of alien plant species of Banks Peninsula. Numbers in parenthesis after each region show the total number of alien species introduced into New Zealand from the region and the percentage present in the flora of Banks Peninsula.

During the last several decades some areas of less intensively managed farmland have been abandoned and left to regenerate back to native shrubland and forest. The present landscape comprises a mosaic of about 10% original or regenerated native forest, 5% native shrubland (less than 6 m tall) and 85% grassland ranging from less-modified areas of semi-native tussock grassland, open shrubland, fernland, sedge and rushland to highly-modified pastures dominated by alien grasses (Wilson, 1994, 1999; Wiser and Buxton, 2008; Wilson, 2009; Wiser and Buxton, 2009).

Given this coexistence of semi-natural and highly managed habitats, Banks Peninsula provides an outstanding opportunity for the development of suitable ecological model systems for analysing the effects of climate, environmental and human-related factors on native and alien plant species composition and structure and richness patterns. Testing the relative importance of various factors (e.g. climate, elevation and land-use) that may drive the invasion process on Banks Peninsula at local-regional scale, and setting this within a global context (i.e. global scale), is the subject of my thesis.

1.4 Native-alien species richness relationship: NARR

An ecological indicator for assessing community invasibility (Levine *et al.*, 2002) can be found in the relationship between native and alien plant species richness (hereafter NARR). This measure, which has been a main focus of ecological research, primarily determines the vulnerability of biological communities to colonization and dominance by introduced species (Fridley, 2011), the vulnerability to invasion (Levine and D'Antonio, 1999; Lonsdale, 1999; Richardson and Pyšek, 2006) and the likelihood of impacts on native species richness (e.g. biotic homogenization; McKinney and Lockwood, 1999; Lambdon *et al.*, 2008; Winter *et al.*, 2009).

While numerous studies have shown that the number of alien species establishing in a community is related significantly to the native species richness of that community [reviewed by Lonsdale (1999)], the strength and direction (whether positive or negative) of the relationship often varies markedly among studies and there is an on-going debate as to whether such variation in the relationship between native and alien species richness can be subsumed under one theory or several (Fridley *et al.*, 2007). Studies that report a negative NARR are usually conducted at small spatial grains (< 100 m^2) and the sign is interpreted as supporting the biotic resistance hypothesis, where competitive effects are strongest and species-rich communities

are more resistant to the establishment of alien plant species than species-poor communities (Elton, 1958; Lodge, 1993; Kennedy *et al.*, 2002). However, other studies have shown the exact opposite, namely a positive NARR, which has been termed the biotic acceptance hypothesis (Stohlgren *et al.*, 2006; Fridley *et al.*, 2007; Bartomeus *et al.*, 2012) because it indicates that sites with high native species richness are the most readily invaded by alien species where native and alien plant species covary with favourable environmental factors (e.g. resource availability, disturbance regime) leading to positive NARR (Levine and D'Antonio, 1999). These contradictory relationships, in the context of a resident native community being invaded by alien species, have been termed the "invasion paradox" (Fridley *et al.*, 2007).

Other important factors, which operate at different spatial grains and extents, might influence the strength and direction of NARR. For instance, at plant-neighbourhood scale, the "Niche Differentiation Hypothesis" (MacArthur and Levins, 1967) might explain the variation in sign and magnitude of NARR; while at large extents (i.e. large ecological gradients) the "Habitat Filtering Hypothesis" (Keddy, 1992) might drive the sign and magnitude of NARR. As well as differing in spatial grain and extent among studies, NARR might be expected to change through time depending on the different invasion stages [i.e. transport, colonization, establishment and spread *sensu* Theoharides and Dukes (2007)] where different factors determine invasion dynamics (Clark and Johnston, 2011; Clark *et al.*, 2013). For instance, Clark *et al.* (2013) demonstrated, via simulation models, that temporal change of NARR may occur in any spatially structured system where species compete for resources and are subject to disturbance. This study showed that a negative NARR occurs when the probability of alien species colonizing an area is inversely related to the density of the native species. In fact, at early stage of invasions, alien species may be advantaged by disturbance while native species may be reduced leading to a negative NARR. In contrast and at a later stage, a positive NARR is the result of both native and alien species responding similarly to the same processes (e.g. disturbance, dispersal and recolonization). Biotic factors such as the number of native and alien species per plot and total species richness may also shape NARR. In an experimental study, Herben *et al.* (2004) showed that the sign and magnitude of NARR varied as a function of mean native and alien number of species per plot. In Chapter 4, I have shown how in the heterogeneous landscape of Banks Peninsula the vegetation structure (and mean native and alien species richness per plot related) determined the changes in the sign of NARR along an elevational gradient. Where, in many areas, more heterogeneity in abiotic conditions together with a net increase in species (i.e.

total species richness) is found, this may also lead to a positive NARR (Stohlgren *et al.*, 1999), although the mechanisms related to NARR for total species richness are not clear (Davies *et al.*, 2005). Abiotic factors such as environmental heterogeneity (i.e. habitat diversity) may also shape NARR. It may be the case that the number of coexisting species in a region is dependent on the magnitude of the habitat diversity within that region (Fridley *et al.*, 2007). Low habitat heterogeneity, limited resources which are completely used and more apparent effects of species competition lead to invasion resistance (i.e. negative NARR; Morgan, 1998; Stachowicz *et al.*, 2002; Fridley *et al.*, 2007). In contrast, high habitat heterogeneity with a diverse species composition and environmental conditions lead to biotic acceptance (*sensu* Stohlgren *et al.*, 2006) with a resulting positive NARR (Levine, 2000; Davies *et al.*, 2005). Covarying factors such as different habitat types, ecosystems and biogeographic regions may also change the sign and magnitude of NARR. For instance, open grasslands as well as riparian/wetlands zones may be more susceptible to invasion than forests due to the availability of light, water and nutrients (Stohlgren *et al.*, 1998, 2002; Maskell *et al.*, 2006; Pyšek *et al.*, 2010a; Fridley, 2011). The NARR may also vary across one or many ecosystems. Darwin (1859) and Elton (1958) suggested that lack of intense interspecific competition on islands made these low-diversity ecosystems more susceptible to invasion compared with mainlands (Gimeno *et al.*, 2006; Pyšek and Richardson, 2006; Stohlgren *et al.*, 2008). Human-related factors (i.e. disturbances) are also likely to be a key contributor to NARR variation (Herben *et al.*, 2004; Fridley *et al.*, 2007). NARR sign and magnitude may change according to land-use history (e.g. positive NARR can be found in young forests converted from agricultural areas; Parker *et al.*, 2010) and land management intensity (e.g. negative NARR in semi-natural wetlands but no significant NARR in highly managed wetlands; Boughton *et al.*, 2011). NARR sign and magnitude may also change within the same landscape depending on the character, magnitude and variation in the dominant environmental or anthropogenic gradients (e.g. positive NARR in alien-dominated but negative in native-dominated communities; Chapter 4). Earlier review articles on NARR (Herben *et al.*, 2004; Fridley *et al.*, 2007) have discussed only a few of these factors (e.g. plot size and extent, native and alien species richness, habitat heterogeneity). Because the NARR has not been adequately quantified so far, gaps still remain in our understanding of NARR.

1.5 Rationale and aims of the project

Several studies have highlighted the importance of quantifying the factors that determine the arrival, initial dispersal, and naturalization of self-sustaining populations, and their spread (Pimentel *et al.*, 2001, 2005; Vilá *et al.*, 2009b; Oreska and Aldridge, 2011) if we are to fully understand and tease apart the drivers of invasion and their ecological and economic implications. Although increasing attention has been given to this matter, it is generally accepted that there is little current knowledge of the factors promoting the naturalization of alien plant species (Duncan and Williams, 2002; Bellingham *et al.*, 2004; Theoharides and Dukes, 2007; Hayes and Barry, 2008; Milbau and Stout, 2008; Diez *et al.*, 2009b). Distribution of alien, and also of native species, are influenced by a number of abiotic (mainly climate) and biotic factors (e.g. water, nutrients or livestock grazing; Pettit *et al.*, 1995; Richardson *et al.*, 2000; Pyšek *et al.*, 2002; Arévalo *et al.*, 2005; Prober and Wiehl, 2012). Successful plant invasion depends not only on the attributes of the invaders (Noble, 1989; Bellingham and Coomes, 2003) but also on aspects on the invaded ecosystem (Catford *et al.*, 2008; Foxcroft *et al.*, 2011; Pyšek *et al.*, 2012). Studies have long determined that some ecosystems contain few alien species (e.g. tropical forests), while others contain many (e.g. warm-temperate regions; Lonsdale, 1999; Pyšek and Richardson, 2006). Focussing on the characteristics of the invaded ecosystem rather than on those of the invader is likely to be a more effective research strategy for understanding the processes of invasion (Hobbs and Humphries, 1995), although Foxcroft *et al.* (2011) have suggested that attention should be paid to both.

Recent studies have advanced hypotheses about the changes in land-use and -management as they covary with climate and which are likely to be major drivers of alien species distribution patterns (Parker *et al.*, 2010), in contrast with native species distribution patterns. However, in a study by Didham *et al.* (2005) that follows MacDougall and Turkington (2005), the authors pointed out how human-related disturbance (e.g. habitat modification) may be the primary driver of native species loss with invasive alien plant species just a passenger. The impact of land-use history and management on the distribution of native and alien species has recently been discussed within the context of invasion ecology in areas such as the United States (Parker *et al.*, 2010; Boughton *et al.*, 2011) and Europe (Polce *et al.*, 2011). Recent biogeographical research has indicated, in fact, that the likelihood of biological invasions at large extents might be reasonably well predicted from an analysis of climatic and bioclimatic factors and human-related impacts, although the interaction

between these two sets of drivers remains unclear (Evans and Gaston, 2005; Evans *et al.*, 2005; Marini *et al.*, 2009; Polce *et al.*, 2011; Marini *et al.*, 2012). Marini *et al.* (2009) tested whether the relationships between species and climatic/bioclimatic factors and between species and human-related factors vary between native and alien species when other environmental variables are taken into account. They concluded that alien species richness was higher in areas with the most rich and diverse assemblages of native species and that there was a stronger response of aliens than natives in currently warm, urbanized, low-altitude areas than in cold, high-altitude areas where human population density was low. Evidence also indicated that the distribution of native and alien plant species across habitats was not similar, with invasive alien species being found more frequently in anthropogenically disturbed habitats (Chytrý *et al.*, 2008b). In a heavily modified landscape, past and recent land use and management may be the primary factors in explaining not only alien species distribution patterns but also those for native species (Chapter 4). These human-related factors may, in fact, promote the establishment of alien species via alterations of the disturbance regime through fire and grazing (Hobbs and Huenneke, 1992; D'Antonio, 2000; Keeley *et al.*, 2003), changes in soil nutrient status as a consequence of fertilization (Dukes and Mooney, 1999; Radford *et al.*, 2010) and increased colonization pressure (*sensu* Lockwood *et al.*, 2009) often by species that are associated with similar human-related disturbances. Hulme (2008, 2009) demonstrated that native and alien plant species distributions may not respond similarly to environmental change. Hulme (2008) highlighted how this outcome is mainly due to the scale dependence of native and alien species distribution according to related climate and environmental factors. Within a region, local environmental drivers (e.g. habitat, propagule pressure and introduction history) influence native and alien species richness differently, while when the spatial grain increases (i.e. across regions), it is climate that influences both native and alien species richness (Hulme, 2008).

My related study therefore seeks to determine how the structure and pattern of native and alien plant communities may be influenced by abiotic and biotic drivers that covary with dominant environmental gradients (i.e. land-use history and management and climate-environmental factors) on the Ecological Region of Banks Peninsula (New Zealand). Disentangling these drivers is an important part of general invasion ecology and is the focus of my particular work.

Geographic Information Systems (GIS) and Remote Sensing (RS) are useful tools in invasion ecology for determining the spatial distribution of (native + alien) plant

species in a heterogeneous landscape such as Banks Peninsula and how this may be best described according to available GIS data layers. In Chapter 2, I use these tools and statistical techniques (i.e. data exploration and validation) to verify both the quality and adequacy of available plant species data and the explanatory variables as GIS data layers which are then used in Chapter 3 and Chapter 4.

Having established in Chapter 2 a body of verified data along with the creation of a geodatabase, I then, in Chapter 3, use multivariate statistical techniques and specific analyses of species composition and structure to determine the interaction of native and alien plant species communities with climate, environmental and human-related factors along the environmental gradients of Banks Peninsula. Understanding how and why native and alien plant species distribution and community structure differ along these gradients with associated human-related factors is the focus of my research in this field of invasion ecology. In order to clarify issues of ordination and classification analysis and to understand if levels of invasion vary across communities in low or highly managed areas, two related questions need to be asked: (1) does invasion lead to distinct native and alien plant communities? and (2) do native and alien dominated communities segregate along abiotic (i.e. climate) or biotic (i.e. land-use history and management) gradients? As species invasions may alter community composition and structure, I then ask if and how alien species influence levels of homogenization and community dissimilarity within and across different plant communities, and how different environmental tolerances of native and alien species shape community structure and nestedness?

The native and alien plant species communities thus established are analysed in Chapter 4 using spatial regression methods to determine the relationship between species richness on Banks Peninsula and abiotic and biotic drivers such as climate, environmental and human-related factors. In this context, it is important to consider the following issues: (1) is the relationship between native and alien plant species richness shaped by variation in anthropogenic and environmental gradients and, if so, how strongly?; (2) do similar native and alien relationships hold in plant communities that have either experienced relatively high or low human impact and are respectively dominated by either alien or native species? and (3) what is the relative contribution of environmental and anthropogenic gradients to the relationship between native and alien plant species richness?

Numerous studies have found that the positive sign of the native-alien species richness relationship (NARR) can be explained by the biotic acceptance hypothesis whereas the negative sign can be explained by the biotic resistance hypothesis

(Stohlgren *et al.*, 2006; Fridley *et al.*, 2007; Bartomeus *et al.*, 2012). However, other studies have suggested that NARR sign and magnitude can be explained by the shift from biotic to abiotic drivers of plant community structure and that this is related to scale dependence of NARR (Fridley *et al.*, 2007). Using the considerable body of international literature on NARR allowed me to examine this apparent contradiction and to examine, in Chapter 5, to what extent NARR on Banks Peninsula might mirror that observed worldwide. Using a meta-analytical approach combined with a multi-model inference within an information-theoretic approach, I also attempt to clarify and explain one of the fundamental questions in plant invasion ecology, that is the variability in the sign and magnitude of NARR at a global scale, the so-called "invasion paradox".

1.6 Nota bene

All chapters have been written as self-contained research papers and therefore some repetition in the introductions, methods and discussions may be found.

Chapter 2, Chapter 3 and Chapter 4 use data which is stored in the Banks Peninsula geodatabase.

Chapter 5 uses a database containing relevant articles personally collected from several sources.

All literature cited in the thesis is given at the end of the thesis.

Chapter 4 has been published as Tomasetto, F., Duncan, R. P. & Hulme, P. E. (2013) Environmental gradients shift the direction of the relationship between native and alien plant species richness. *Diversity and Distributions*, 19:49-59. See Appendix K.

Chapter 2

Banks Peninsula geodatabase

"GIS, Remote Sensing and spatial analysis techniques are paving the way for very detailed and novel studies of invasion patterns and processes."
(David M. Richardson)

2.1 Abstract

The study of the distribution of plant species in relation to the spatial distribution of environmental predictors is essential in ecology and can be divided in two phases: data gathering and analysis. In this chapter, I focus on phase one and using GIS and spatial analysis I investigate: (1) which available GIS data layers may best describe a heterogeneous landscape such as Banks Peninsula (New Zealand) in the context of plant species distribution patterns; (2) which sampling methods (systematic, random and equal-stratified) can best provide a representative sample of the variation in climate, environmental and human-related factors across the Peninsula; (3) using the data sampled by the best sampling approach, if there is a protocol for data validation and exploration that avoids potential statistical violations. GIS automated workflows generated relevant data layers. Based on the results of the tests such as the variance ratio *F* test and Wilcoxon rank-sum test, it was possible to rank the sampling methods for accuracy according to the following sequence: Systematic > Stratified > Random. A series of problems (i.e. outliers, colinearity, non-normality and spatial autocorrelation) was encountered in the data exploration of the systematic sampling approach. However, I identified a protocol that dealt with these issues and reduced the chance of drawing incorrect conclusions from the data and analysis.

Keywords: GIS, Remote Sensing, plant invasion, sampling design, data exploration.

2.2 Introduction

The need to understand the dynamics of species distributions in space and time is essential in ecology, and in particular in biological invasions where the spatial pattern of invasion is specific to a time, space and spatial scale (Theoharides and Dukes, 2007). To understand plant species patterns (e.g. composition and richness) in relation to the spatial distribution of environmental factors, two phases are required: data gathering and analysis. In this chapter, I focus on the data gathering that takes

the form of a floristic survey that defines the area of investigation and the potential environmental factors that may characterize this area.

The Banks Peninsula comprehensive floristic survey was designed to find out as much as possible about the vegetation cover and species distribution patterns on the Peninsula (Wilson, 1992). But, if we are to fully understand species patterns within this area we need also to collect data on factors that might affect species distributions. The larger and more diverse the study area is the larger and the more variable is the dataset necessary for an adequate representation of its vegetation (so-called ecological representativeness; *sensu* Stohlgren *et al.*, 2003b; Rew *et al.*, 2006; Roleček *et al.*, 2007). Because factors underpinning plant species distributions patterns operate at different spatial and temporal scales (Collingham *et al.*, 2000), it is essential to identify their relative importance and emphasize a congruent spatial scale between the resolution of species and environmental factors. Bearing in mind this, there is often issues of discrepancy between map or layer resolution and spatial scales at which the ecological studies is conducted. In fact, environmental factors are usually available at a relatively coarse scale, but other factors (e.g. geological and lithological maps, soil moisture or soil nutrient content) may vary substantially on a much finer grain or be unknown (Roleček *et al.*, 2007). To deal with this, we need to emphasize a congruent spatial scale between the resolution of species and environmental factors. Spatial scale is in fact important to both species distribution and related environmental data (Elith and Leathwick, 2009). When studying their relationship, it is important that the grain (i.e. grid cell or polygon size) of the explanatory variables is consistent with the species data layers (Elith and Leathwick, 2009). However, in most cases around the world, as in Banks Peninsula, this kind of consistency is difficult to find.

For this, Geographic Information Systems (GIS), Remote Sensing (RS) and spatial analysis techniques are useful tools in landscape ecology and biogeography, as well as in invasion ecology. GIS and RS have emerged as distinct spatial data handling technologies with their own methods of data representation and analysis (Goodchild, 1994). These technologies have attracted considerable interest in the field of modelling of plant species distribution in recent years. In the context of plant invasions, "these are paving the way for very detailed and novel studies of species patterns and processes" (Richardson, 2004). Integrated GIS and RS have been successfully applied to detect and map the distribution of several alien plant species (e.g. Dark, 2004; Rew *et al.*, 2005; Higgins *et al.*, 1999; Evangelista *et al.*, 2009), their spatial dynamics (e.g. Underwood *et al.*, 2004; Müllerová *et al.*, 2005;

Bradley and Mustard, 2006; He *et al.*, 2011), their ecosystems (e.g. Deutschewitz *et al.*, 2003), their bio-climatic conditions (e.g. Rouget *et al.*, 2004) and the drivers affecting invasions (e.g. Rouget and Richardson, 2003; Foxcroft *et al.*, 2004; Pino *et al.*, 2005). For instance, climate, environmental (e.g. topography) and potential human-related disturbance (e.g. land-use and propagule pressure) have been shown to influence alien species (e.g. Rouget and Richardson, 2003; Pino *et al.*, 2005) and native species distribution (Deutschewitz *et al.*, 2003; Dark, 2004).

The ability to analyse, map and model plant species are just a few of the many advantages of using GIS and RS for this work. These technologies contribute to our understanding of the width dynamics of species patterns, and integrated with spatial analysis allow us to design objective, efficient sampling methods (e.g. random, systematic or stratified) and/or to evaluate their adequacy in capturing species and environment (Neldner *et al.*, 1995). We tend to evaluate sampling methods especially when the study area is large and cannot be entirely sampled (Rew *et al.*, 2006). For instance, opportunistic sampling method (i.e. samples collected from known localities or in easily accessible areas) may be preferred to unbiased methods *sensu* Rew *et al.* (2006), such as random or stratified random sampling, but the latter may fail to capture the spatial variation or spatial dependency of the environment, leading to difficulties in detecting spatial relationships or incorrectly inference statistical models (Legendre *et al.*, 2002; Fortin and Dale, 2005).

To achieve a representative sample of the population (e.g. the Banks Peninsula vegetation), the appropriate theories to guide sample design need to be based on an understanding of the geographical structure and ecological organization of plant communities with regard to the heterogeneity of the sampled vegetation type (Huebner, 2007) or the environments associated with species occurrence (Stohlgren *et al.*, 2003b). For instance, an opportunistic sampling method is useful in defining the breadth of environmental conditions that characterize each species location (i.e. environmental envelope; Jarnevich *et al.*, 2007; Evangelista *et al.*, 2008). However, this non-objective sampling method has some limitations such as over-estimating species presence or missing species presence in localized random samples (Stohlgren and Schnase, 2006; Fitzpatrick *et al.*, 2009).

In this chapter, I describe the GIS, RS operations and tools, and spatial analysis techniques I used to analyse the range of environments on Banks Peninsula associated with the floristic survey and to ask:

1. In this highly variable landscape, how can plant species distribution be best described using available spatial data?

2. Is a systematic sampling scheme suitable for providing a truly representative picture of the Banks Peninsula environments?
3. Do the environmental variables extracted using this sampling approach violate any statistical assumptions?

2.3 Materials & Methods

2.3.1 Study area

Banks Peninsula (*c.* 1000 km^2) on the south-east coast of the South Island, New Zealand (between 43°33' - 43°54' S and 172°37' - 173°7' E), comprises the eroded remnants of two large shield volcanoes, creating a highly varied topography that ranges from sea level to 920 m above (Mt Herbert). Climate and soils of Banks Peninsula form a complex pattern. At a regional landscape-scale, climatic conditions are influenced by the prevailing north-easterly wind flowing across the South Island (Wilson, 2009); at local scale, the diverse topography of the Peninsula and the effect of the open ocean influence the climate (Wilson, 1992). Annual rainfall ranges from 600 mm at the driest low elevation sites to 2000 mm at some higher elevation sites, and a mean daily temperature ranges from 8 to 13°C. In combination with this fluctuating climate the surface of the landscape is constantly eroded by *c.* 38 km of permanent rivers (large natural permanent flowing water bodies) or *c.* 1228 km of streams (perennial or intermittent tributaries of permanent rivers) that descend the main valleys and gullies. Soils are derived from basaltic volcanic rock and loess (Sewell *et al.*, 1992), and are typically well drained and of moderate to high fertility (Speight, 1943; Williams, 1983; Sewell *et al.*, 1992; Wilson, 2009).

Banks Peninsula is also characterized by strong gradients in land-use history and management, and distribution of human population. The present landscape comprises a mosaic of about 10% original or regenerated native forest, 5% native shrub (less than 6 m tall) and 85% grassland ranging from less-modified areas of semi-native tussock grassland to highly-modified alien pastures (Wilson, 1994, 1999). This gradient in vegetation, from native forest to shrubland to semi-native tussock grassland to alien-dominated pasture, covaries with elevation but principally reflects a gradient in human-related impacts, from sites less modified by burning, grazing, fertiliser addition and oversowing of improved alien pasture species to sites that have been heavily modified by these processes. In addition, human population density is low in the region, with approximately 7000 people living on the Peninsula largely

concentrated in three major settlements: Akaroa, Diamond Harbour and Little River (Statistics New Zealand, 2006). There is an extensive road network on the Peninsula both paved (*c.* 589 km) and unpaved roads (*c.* 313 km).

2.3.2 Plant species data

The data from the Banks Peninsula comprehensive floristic survey, conducted between 1983 and 1988, were originally used in a Protected Natural Areas (PNA) Programme report (Myers *et al.*, 1987) describing Recommended Areas for Protection (RAPs) within the Banks Peninsula Ecological Region (Wilson, 1992). The species composition of all vascular and non-vascular plant species was recorded within each of more than 1300 6 × 6 m plots at each intersection of a regular 1000 × 1000 yard grid (*c.* 920 × 920 m) drawn over the entire Banks Peninsula and Ellesmere/Kaitorete spit and each species was ranked according to its relative abundance in the plot (Figure 2.1 and Appendix A). For this thesis, I considered only the Banks Peninsula as study area and only vascular plant species and excluded 33 plots without any vascular species, leaving a total of 1227 plots. Plant species were classified as native or alien to New Zealand following the standard definitions [New Zealand Plant Names database - available at http://nzflora.landcareresearch.co.nz ; Parsons *et al.* (1995); Mahon (2007)]. Species nomenclature follows *Flora of New Zealand* (Moore and Edgar, 1970; Healy and Edgar, 1980; Allan, 1982; Webb *et al.*, 1988; Edgar and Connor, 2000). The 36 m^2 plot size is consistent with recommendations for adequately sampling grassland vegetation in New Zealand (Hurst and Allen, 2007) and Europe (Chytrý and Otýpková, 2003; Otýpková and Chytrý, 2006). I calculated the total number of native and alien species per plot, which I used as response variables (Chapter 4) or I transformed the relative abundance of native and alien species in the plot into its arbitrary percentage values (i.e. 0-100%) using the function *vegtrans* contained in the *labdsv* package Roberts (2012), which I then used as response variables (Chapter 3). This specific transformation allows direct algebraic transformation (e.g. logarithm) of the vegetation data (Roberts, 2012). I classified each plot as either 'native dominated' or 'alien dominated' based on whether the species ranked as the most abundant in each plot was native or alien, respectively. I further classified each species as a tree (woody species $\geq$ 6 m tall), shrub (woody species $<$ 6 m tall including lianes), fern, herb or grass following trait categories database (Ecological Traits of New Zealand Flora - available at http://ecotraits.landcareresearch.co.nz/) and calculated the relative proportions of these groups in each plot.

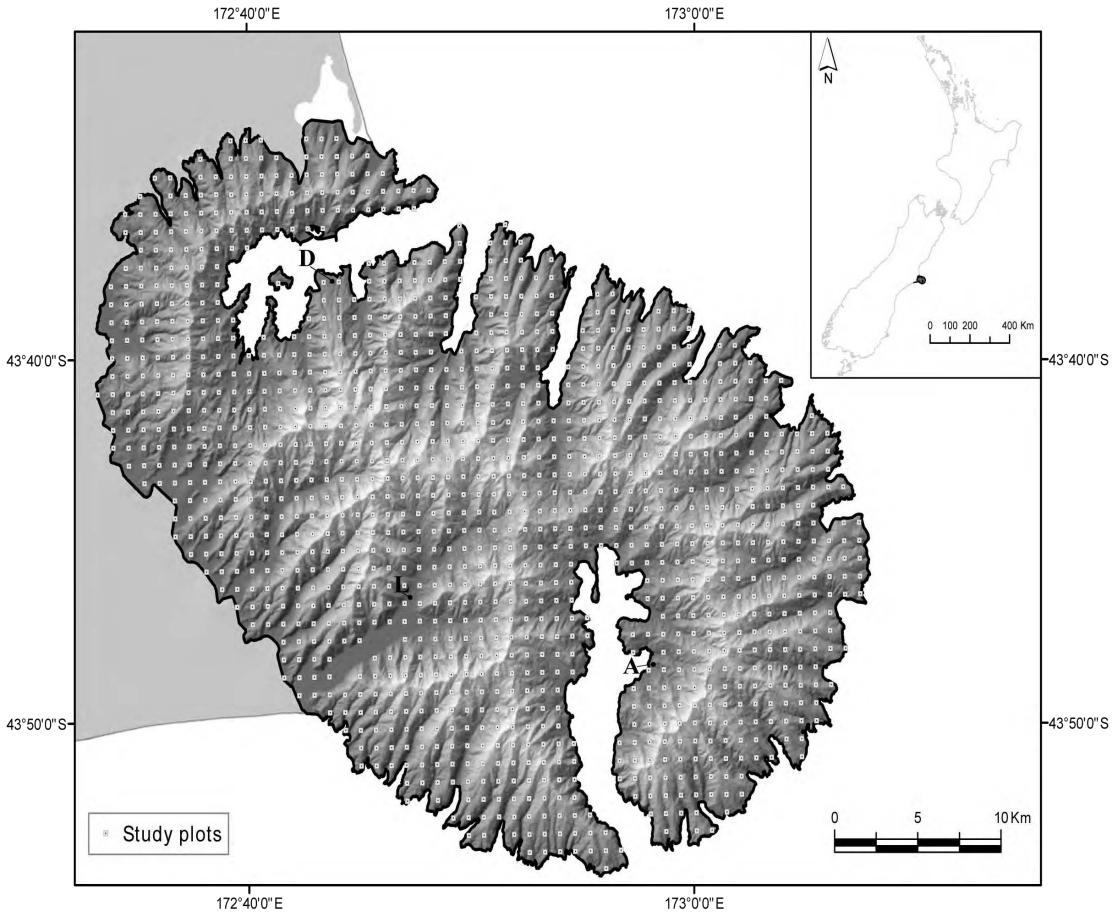

Figure 2.1. Schematic map of Banks Peninsula (*c.* 1000 Km^2), its location in New Zealand (inset) and details of the vegetation sampling design. The 1227 study plots (36 m^2) are illustrated by the grid of grey points. Location of major towns are as follows: A - Akaroa, D - Diamond Harbour and L - Little River.

2.3.3 Processing spatial data layers

Bearing in mind that the complex Banks Peninsula landforms are associated with strong gradients of climate, land-use history and management along with the distribution of human population, I broke the objectives of this study down into measurable criteria and relevant data requirements. I then built a GIS geodatabase that contains plant species data and potential explanatory variables in the form of spatially explicit data layers within the extent of the Banks Peninsula floristic survey. Data were created and modified *ad hoc*, stored and extracted using ArcGIS 9.3 software (ESRI, 2009) and Earth Resource Data Analysis System software (ERDAS IMAGINE 9.1; Leica and Geosystems, 2008). GIS and RS final results (output data and maps) are included in a folder at this thesis link (Appendix B) for further consultation.

In the GIS environment, spatial analysis (i.e. GIS tools) and geoprocessing (i.e. modelling the spatial analysis) involved a systematic methodology and sequence of operations (i.e. managing geographic data and performing analysis) with the aim to best evaluate and interpret the results (e.g. output data or map views). For this part of the thesis, I developed a GIS model with customized workflows using the ModelBuilder application in ArcGIS 9.3, a large suite of tools and operations which I then used to build the Banks Peninsula geodatabase (Figure 2.2). I selected a first set of 20 available variables classified as:

- climatic and bioclimatic data
- human-related data
- environmental data (i.e. hydrographical and topographical).

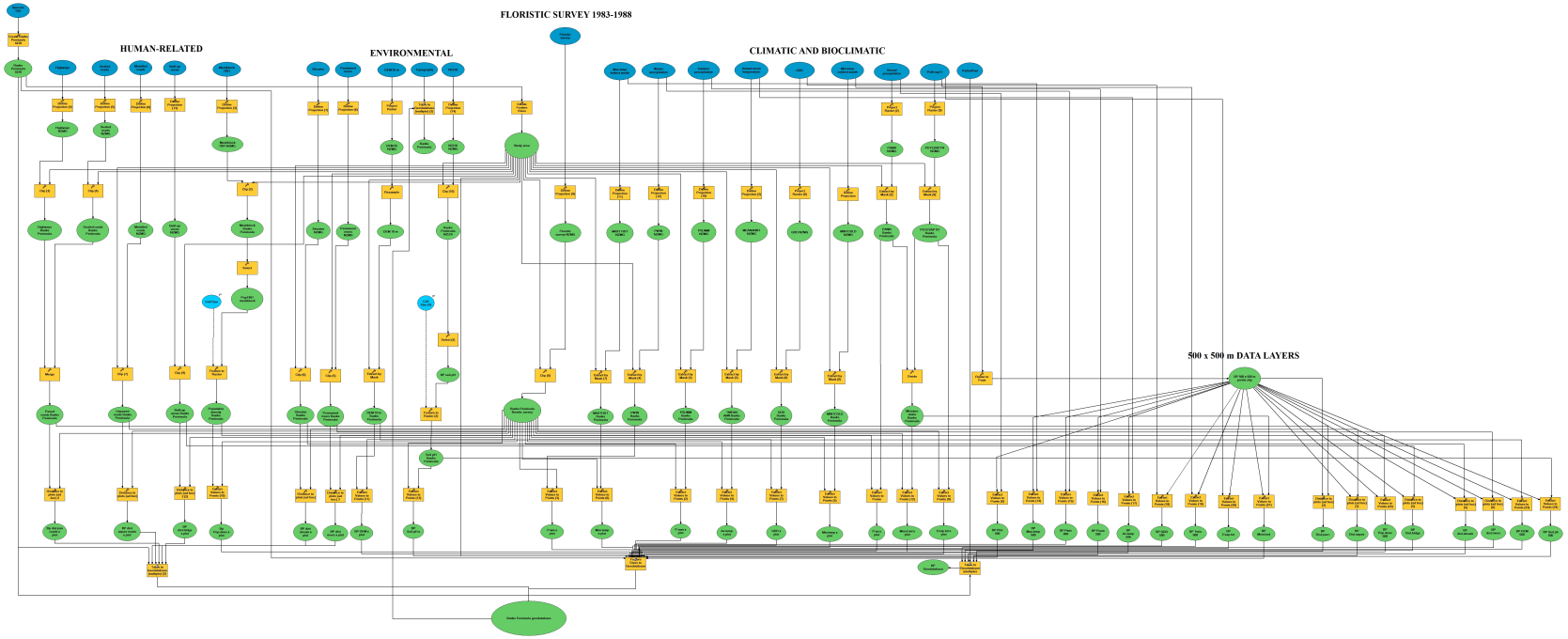

Figure 2.2. GIS model from the Banks Peninsula geodatabase using ModelBuilder application in ArcGIS 9.3. Blue = input data; yellow = GIS tools; green = output data.
Note: the size of this figure is such that, when reduced to A4 size the clarity of the details in the figure suffers. A fully clear figure is produced in A3 paper size and it is attached to the hardbound copy of this thesis (Figure R.1).

All of these data could potentially explain the pattern of plant species [Table 2.1 and Table 2.2; (e.g. Zimmermann and Kienast, 1999; Carboni *et al.*, 2010; Barni *et al.*, 2011; De-Albuquerque *et al.*, 2011)]. For each plot (using the plot centre), I extracted the values of the listed variables ensuring that points did not lie on grid cell boundaries. For the distance-related data, I calculated the distance (m) of each point to variables such as built-up area (or buildings), paved or unpaved roads, rivers and streams. For all these data, I used a Visual Basic for Applications (VBA) script integrated with a Python script (available at http://www.ian-ko.com/) that I executed using ArcGIS 9.3 (Appendix C).

All data were projected from New Zealand Geodetic Datum 1949 (NZGD1949; Lee, 1978) to New Zealand Map Grid (NZMG; Reilly, 1973) to facilitate overlay of all the GIS data layers.

Table 2.1. Characteristics of 20 explanatory variables calculated for the 4108 points Banks Peninsula reference dataset. Abbreviations: Unit = units of measurement; Type = variables classified as continuous (cont.); Resolution = spatial resolution of GRID maps; Year/Period of measurement; descriptive statistics and data sources. Acronyms are defined in the abbreviations page list.

	Unit	Type	Resolution	Year / Period	Min	Max	SD	Source
CLIMATIC VARIABLES								
Total annual precipitation (P.tot)	mm	cont.	500 × 500 m	1971 - 2000	628.19	1998.75	266.71	NIWA
Summer precipitation (P.sum)	mm	cont.	500 × 500 m	1971 - 2000	121.08	368.81	47.94	NIWA
Winter precipitation (P.win)	mm	cont.	500 × 500 m	1971 - 2000	258.21	715.32	100.33	NIWA
Annual mean temperature (Av.temp)	°C	cont.	500 × 500 m	1971 - 2000	8.97	13.32	0.88	NIWA
BIOCLIMATIC VARIABLES								
Minimum temperature of the coldest month (Min.temp)	°C	cont.	500 × 500 m	1971 - 2000	1.85	5.76	0.77	NIWA
Maximum temperature of the hottest month (Max.temp)	°C	cont.	500 × 500 m	1971 - 2000	18.46	23.91	1.06	NIWA
Growing degree days above 5°C (GDD)	-	cont.	500 × 500 m	1971 - 2000	1522	2889	268.83	NIWA
Potential evapotranspiration (Evap.tot)	kJ × °C	cont.	500 × 500 m	1971 - 2000	1.45	2.05	0.13	NIWA
Moisture index (Moist.ind)	mm / kJ °C	cont.	500 × 500 m	1971 - 2000	2496.34	20337.98	2578.92	NIWA
Potential solar radiation (Sol.rad)	kW/m^2	cont.	-	-	0.29	0.98	0.14	R script
HUMAN-RELATED VARIABLES								
Human population density (Pop.dens)	Ab. / m^2	-	-	1991	0	351	42.66	Statistics NZ
Distance of the plots to buildings (Dist.bldgs)	m	cont.	-	-	0	9518.41	2081.32	LINZ
Distance to paved roads (Dist.pav.road)	m	cont.	-	-	0.25	6770.52	1248.46	GIS
Distance to unpaved roads (Dist.unpav.road)	m	cont.	-	-	0.2	4312.05	855.21	GIS
ENVIRONMENTAL FACTORS								
Distance to rivers (Dist.rivers)	m	cont.	-	-	2.91	18853.82	4264.66	NZ REC
Distance to streams (Dist.streams)	m	cont.	-	-	1	2304.95	196.92	NZ REC
Elevation (DEM)	m	cont.	10 × 10 m	-	0	920	181.38	GIS
Aspect	-	cont.	-	-	0	358.53	105.55	Field measure
Slope	%	cont.	-	-	0	59.92	9.85	Field measure
Mean soil pH (soil.pH)	-	cont.	-	-	5.21	7.42	0.36	NZLRI

Table 2.2. Summary statistics of 20 explanatory variables calculated in 4108 points that describe the Banks Peninsula environments.

	Mean	SD	Skew	Kurtosis	SE
P.tot	1239.57	266.71	-0.05	-0.77	7.62
P.sum	263.06	47.94	-0.46	-0.24	1.37
P.win	501.57	100.35	-0.41	-0.91	2.86
Av.temp	11.67	0.88	-0.48	-0.53	0.03
Min.temp	3.63	0.77	0.31	-0.28	0.02
Max.temp	21.84	1.07	-0.41	-0.55	0.03
GDD	2315.88	268.83	-0.42	-0.59	7.71
Evap.tot	1.83	0.13	-0.45	-0.66	0
Moist.ind	7730.14	2578.92	0.95	1.83	73.62
Sol.rad	0.74	0.14	-0.58	-0.21	0
Pop.dens	67.52	42.66	6.24	44.51	0.77
Dist.bldgs	2970.61	2081.31	0.94	1.52	32.91
Dist.pav.road	1393.16	1248.46	1.14	0.91	34.97
Dist.unpav.road	1121.91	855.21	0.84	0.09	24.58
Dist.rivers	6697.75	4264.66	1.67	2.79	51.79
Dist.streams	261.89	196.92	2.88	15.28	6.02
DEM	256.07	181.56	0.61	-0.39	5.18
Aspect	183.65	105.59	-0.07	-1.24	3.01
Slope	19.29	9.85	0.21	-0.21	0.28
Soil.pH	5.64	0.36	0.91	1.09	0.01

2.3.4 Climate and bioclimatic layers

I estimated the values of climate data from climatic maps in GRID format of 500 × 500 m resolution, obtained from the National Institute of Water and Atmospheric Research (NIWA) in Wellington, New Zealand. Those maps were generated by interpolating precipitation and temperature data recorded in 500 meteorological stations and calculated as average of the 1971 - 2000 period using the spline model ANUSPLIN (Version 4.3; Hutchinson, 2007). Using a trivariate thin plate smoothing spline model, Tait and Zheng (2007) have produced several climate parameters (available at http://www.niwa.co.nz/our-science/climate/our-services/mapping). This spline method appeared to capture the main features of New Zealand's rainfall (i.e. topographic enhancement, rain shadow and coastal versus inland differences) and has been shown to perform well in the variable New Zealand topography (Tait *et al.*, 2006). For temperature-related data, Tait *et al.* (2006) used two independent

fixed variables (latitude and longitude) and as a third the Digital Elevation Model (DEM). The latter variable was substituted by 1951-1980 mean annual rainfall for rainfall-related data. I chose climate variables that are considered to influence the growth and distribution of plant species (e.g. Collingham *et al.*, 2000; Barni *et al.*, 2011; De-Albuquerque *et al.*, 2011), being aware of the scale-dependence of processes that determine species distribution patterns (Collingham *et al.*, 2000).

I used climate variables (Table 2.1) such as:

- Total annual precipitation
- Summer precipitation
- Winter precipitation
- Annual mean temperature.

I also used bioclimatic variables (i.e. variables derived from the monthly temperature and rainfall values in order to generate more biologically meaningful variables *sensu* BIOCLIM available at http://www.worldclim.org/bioclim) such as:

- Minimum temperature of the coldest month
- Maximum temperature of the hottest month
- Growing degree days above 5°C [as a surrogate for evapotranspiration and calculated as the sum of average daily temperature minus 5°C; Healy and Scanlon (2010)].

In addition in the geodatabase, I included climatic raster maps of Moisture index (Mi; UNEP, 1992) and potential evapotranspiration. The Moisture index is based on:

$$\mathrm{Mi} = \mathrm{P}/\mathrm{Etp}$$

where P is the mean annual precipitation, Etp is the potential evapotranspiration.

I also quantified potential solar radiation, as a measure of the amount of radiation per unit area reaching earth's surface as a proportion of the amount received at the equator. I calculated those values using a script (Kaufmann and Weatherred, 1982) in R environment (R Development Core Team, 2012) derived from latitude, aspect and slope which were assessed directly on each plot by Hugh Wilson.

2.3.5 Human-related layers

Since human population density may be a proxy measure for propagule pressure and disturbance (Hulme, 2008; Botham *et al.*, 2009), I quantified human population density using the *1991 New Zealand Census* book (Statistics New Zealand, 1991). I obtained this layer by integrating data from the non-digitalized *1991 Census books* with 1991 meshblocks vector data layer (the smallest geographic area for which statistical data is collected and processed; Statistics New Zealand definition). Built-up areas were classified as areas with at least three houses or other buildings in an area of at least 1.012 ha (U.S. Geological Survey Land Cover Institute definition). To identify and produce further information about the built-up areas, I georeferenced (using ground control points) and photointerpreted nine orthorectified aerial photographs from the early 1990s (2.5 × 2.5 m spatial resolution) of Banks Peninsula derived from Land Information New Zealand (LINZ; available at http://www.linz.govt.nz/). To ensure accuracy of the locations of built-up areas from the aerial photographs, I undertook field verification.

Previous studies have found that roads may be important conduits of alien plant dispersal and suitable habitats for many alien plant species (McKinney, 2002; Arévalo *et al.*, 2005; Sullivan *et al.*, 2009; Aikio *et al.*, 2012). Sullivan *et al.* (2009) have demonstrated that New Zealand's reserves adjacent to roads had significantly higher weed richness than reserves further from roads, although the causal mechanisms are unclear. Accordingly, I classified the road network across the Peninsula as paved (i.e. highway or sealed road) or unpaved roads.

2.3.6 Environmental layers

Wilson (2008) highlighted that the main valleys and gullies on Banks Peninsula are characterized by permanent rivers and flowing streams, providing higher soil-moisture conditions and less disturbance than the surrounding open ground. However, riparian areas are known to be highly vulnerable to invasion by alien species, especially when subjected to human-induced disturbances (Aguiar *et al.*, 2001; Parks *et al.*, 2005). Thus, to better understand the plant species patterns in those habitats, I included in the geodatabase permanent rivers or streams, as defined in the New Zealand River Environment Classification (REC; Snelder *et al.*, 2010).

I obtained elevation data from a DEM at 25 m spatial resolution downscaled to a resolution of 10 m by using geostatistical analysis that directly incorporated auxiliary maps (i.e. all GIS layers that can explain spatial distribution of measured elevations

and associated errors) following Hengl *et al.* (2008) and using *sp* (Pebesma and Bivand, 2005; Bivand *et al.*, 2008) and *gstat* (Pebesma, 2004) packages. As auxiliary maps, I considered the distance of each plot to streams. I assessed the accuracy of the downscaled DEM using cross-validation and root mean-squared error (RMSE) at selected ground control points (Appendix D). I also integrated this data with physiographic measures (such as aspect and slope) which were measured directly on each plot by Hugh Wilson. This may allow an accurate representation of the surface of the entire Banks Peninsula avoiding any underrepresentation of steep slopes.

I produced a mean soil pH (measured at 0.2 - 0.6 m depth) data layer obtained from a soil unit polygon layer delineating physiographic areas contained in the New Zealand Land Resource Inventory (NZLRI database; Landcare Research NZ Ltd., 2000) and integrated with the National Soils Database (NSD; Wilde, 2003).

From the NZLRI database, I also extracted land-cover and land-use data layers obtained from a polygon layer delineating physiographic areas defined either physiographically or on the basis of vegetation differences contained in an inventory of different vegetation cover classes. However, after I verified the accuracy of the data and found out that there were major discrepancies between the land-cover classes detected by the NZLRI and by the 1983-1988 field survey I did not include this data layer in the final Banks Peninsula geodatabase.

I also georeferenced and photointerpreted a geological map (Institute of Geological and Nuclear Sciences, 1983, scale 1:100000) to produce simplified information and classification about the lithological conditions on Banks Peninsula already present in a polygon layer derived from stereo photograph interpretation, field verification and measurement as part of the 1:63000/1:50000 scale in New Zealand Resource Inventory. However, I did not include this data layer in the final Banks Peninsula geodatabase because of its colinearity with mean soil pH ($rho > 0.5$), but I have made it available for future analysis in a folder at this thesis link (Appendix B).

2.3.7 Statistical analysis

2.3.7.1 Sampling methods

Because designing an efficient sampling strategy is of crucial importance when studying the distribution of a species in relation to the spatial distribution of environmental predictors (Hirzel and Guisan, 2002; Rew *et al.*, 2006) and in order to establish the background environmental conditions for my study, I estimated the values of climatic and bioclimatic, human-related and environmental variables for each centre

point location ($n = 4108$) drawn over the intersection of a regular 500 × 500 m grid that may be used to describe the Banks Peninsula environments (reference dataset). The choice of this spatial resolution was mainly dictated by the resolution of the raster climatic maps available and this also allowed me to avoid the unnecessary introduction of noise and bias (Zandbergen, 2010). I estimated those variables for each plot location from the systematic sampling survey (920 × 920 m spatial resolution).

I then tested and compared the 1983-1988 systematic sampling method with different, unbiased and most commonly used sampling strategies (Rew *et al.*, 2006), such as random sampling and equal-stratified sampling in order to determine which of the three sampling methods could best detect the variation of the whole Peninsula environments (reference dataset). To do so, I tested if the sample variances (using the variance ratio; *F*-test), and means (using Wilcoxon rank-sum test, W) obtained from the three sampling methods were significantly different from the ones of the reference dataset. These test methods are well established in the literature [see Rew *et al.* (2006)].

A standard random sampling scheme would be composed of sample points that are located across the Peninsula completely at random and then the relevant data layers extracted for each of these points. In my case, the random sampling included a set of 1227 points selected at random based on the sampling from the more than 4000 points of the regular grid used to describe the Banks Peninsula environments (i.e. reference dataset). The choice of this "restricted" random sampling method was mainly driven to avoid the unnecessary introduction of noise and bias (Zandbergen, 2010) as might occur in a "truly" random sampling method. I repeated the random selection of this subset of the reference dataset (i.e. 1227 points) for 10000 times (i.e. permutations) and estimated the variances and means of explanatory variables extracted for each of these points.

For the equal-stratified sampling, I used *strata* function in the *sampling* package (Tillé and Matei, 2012) following the methodology of Hirzel and Guisan (2002). I selected four stratifying variables (total annual precipitation, 1991 population density, distance to streams and elevation) among those supposed to be more meaningful for their influence on the distribution of species. Remaining variables were split into four classes each of those containing the selected stratifying variables. The study area was then partitioned by combining these classes to generate 11 (at most) homogenous strata. I then randomly sampled without replacement an identical

number of points in each stratum up to a total of 1227 points in which I estimated each of the explanatory variables.

Although further sampling schemes, such as road-based sampling (e.g. road-based sampling; Pauchard and Alaback, 2004; Arévalo *et al.*, 2005; Arteaga *et al.*, 2009) may be time-efficient and effective, these may sample only for species with restricted distribution along the roads (Maxwell *et al.*, 2012) or may bias the sampling by their locations which generally follow hilltops and valleys, thus leaving significant areas unsampled. For these reasons, I did not included them in the analysis.

2.3.7.2 Data validation and exploration

In order that common statistical problems may be avoided *sensu* Zuur *et al.* (2010), I undertook data exploration of the explanatory variables that characterize the Banks Peninsula environments. These were derived from the "best" sampling approach. Other sampling methods did not provide useful information in the context of Banks Peninsula and therefore were not tested (see Results). Specifically I tested for:

1. data errors (i.e. outliers) using a graphical tool (Cleveland, 1993), a function contained in the *AED* package (Zuur, 2010)

2. normality distribution using *nortest* package (Gross, 2012). I assumed that the data were non-normally distributed, thus I did not make use of any parametric tests. Consequently, as a non-parametric test I used the Lilliefors (Kolmogorov-Smirnov) test. Although this test statistic is the same as that obtained from Kolmogorov-Smirnov test (when mean and variance are not specified), it is not correct to use the *P*-value from the latter for the composite hypothesis of normality (i.e. any hypothesis which does not specify the population distribution completely), since the distribution of the test statistic is different when the parameters are estimated

3. multicolinearity using Spearman's rank correlation matrix, because this measure is less sensitive and more robust than Pearson's correlation to outliers. I also used Variance Inflation Factors test (Fox and Weisberg, 2011)

4. spatial autocorrelation using the Monte Carlo randomized permutation test (n = 10000) for Global Moran's I contained in the *spdep* package (Bivand *et al.*, 2011), because the presence of spatial autocorrelation may alter the parameter estimates and error probabilities of any statistical models by influencing the variance-covariance matrix (Kühn, 2007). To graphically analyse spatial autocorrelation for all selected explanatory variables, I calculated geodesic distances between plots using the latitudinal and longitudinal data based on the centre point location.

It is worth mentioning here that in Chapter 3, I also used another data exploratory test to fit selected explanatory variables in a multivariate analysis such as Non-Metric Multidimensional Scaling technique (NMDS). This enabled me to explore what the major axes of variation are in my data.

2.4 Results

The resulting comparison of sampling methods is summarised in Figure 2.3, Figure 2.4, Figure 2.5. The choice of the climatic and bioclimatic, human-related and environmental variables that have been tested ($n = 11$) and used in the Chapter 3 and Chapter 4 are based on the results of a Spearman's rank correlation matrix, VIF analysis (Table 2.3, Table 2.4 and Table 2.5) and on the criteria that the variables are an unbiased estimate of the Banks Peninsula environments (see below).

Based on the results of the F-test and Wilcoxon rank-sum test, it was possible to rank the accuracy of the methods according to the following sequence: Systematic > Stratified > Random. For these datasets, the systematic sampling survey resulted in the most accurate method to detect the variation of the whole Peninsula environments, there being significant differences in the test statistics for only two out of 11 selected explanatory variables. In this sampling method, population density and distance to rivers were, in fact, significantly lower (5.1 ± 0.7 and 2040.2 ± 51.8 respectively) than for the figures from the > 4000 points Banks Peninsula reference dataset (67.5 ± 0.7 and 6697.8 ± 66.5, $W = 230347.5$ and 745258, $P < 0.001$, respectively). In contrast the equal-stratified design showed more accuracy than the random sampling method in detecting the Peninsula environments but with over- or under-estimation values for several variables ($n = 4$ and 11, respectively).

Using Cleveland dot plots as a graphical tool (Appendix E), I found that for the Moisture index there were eight outlier points; for human population density ($n =$

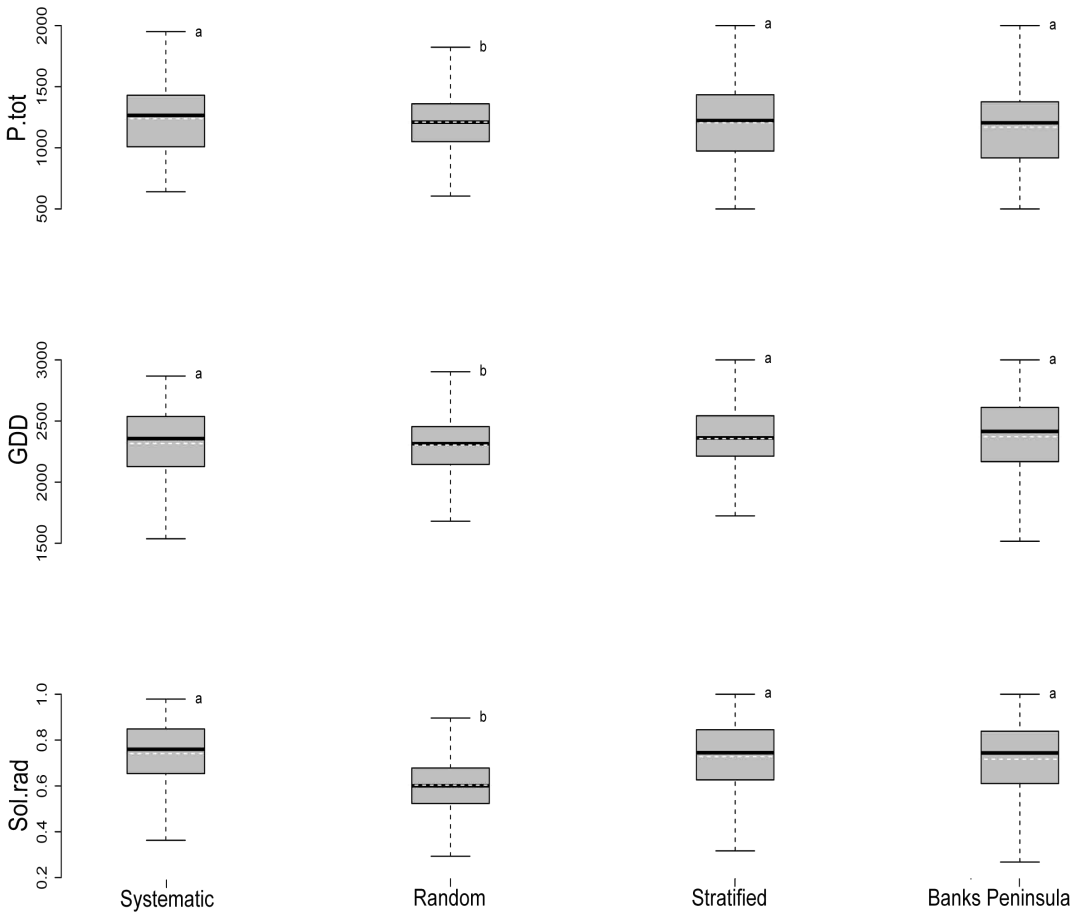

Figure 2.3. Box and whisker plots showing variation around the median of the climatic variables using three different survey methods. The random and stratified sampling methods were generated using a regular grid of 500 × 500 m as well as the Banks Peninsula data (used to approximate the variation of the whole study area). Solid black lines within grey box represent the median; dashed white lines the mean; whiskers represent the 10th and 90th percentiles. Different letters above the boxes indicate significant differences ($P < 0.001$) in the F-test and Wilcoxon test.

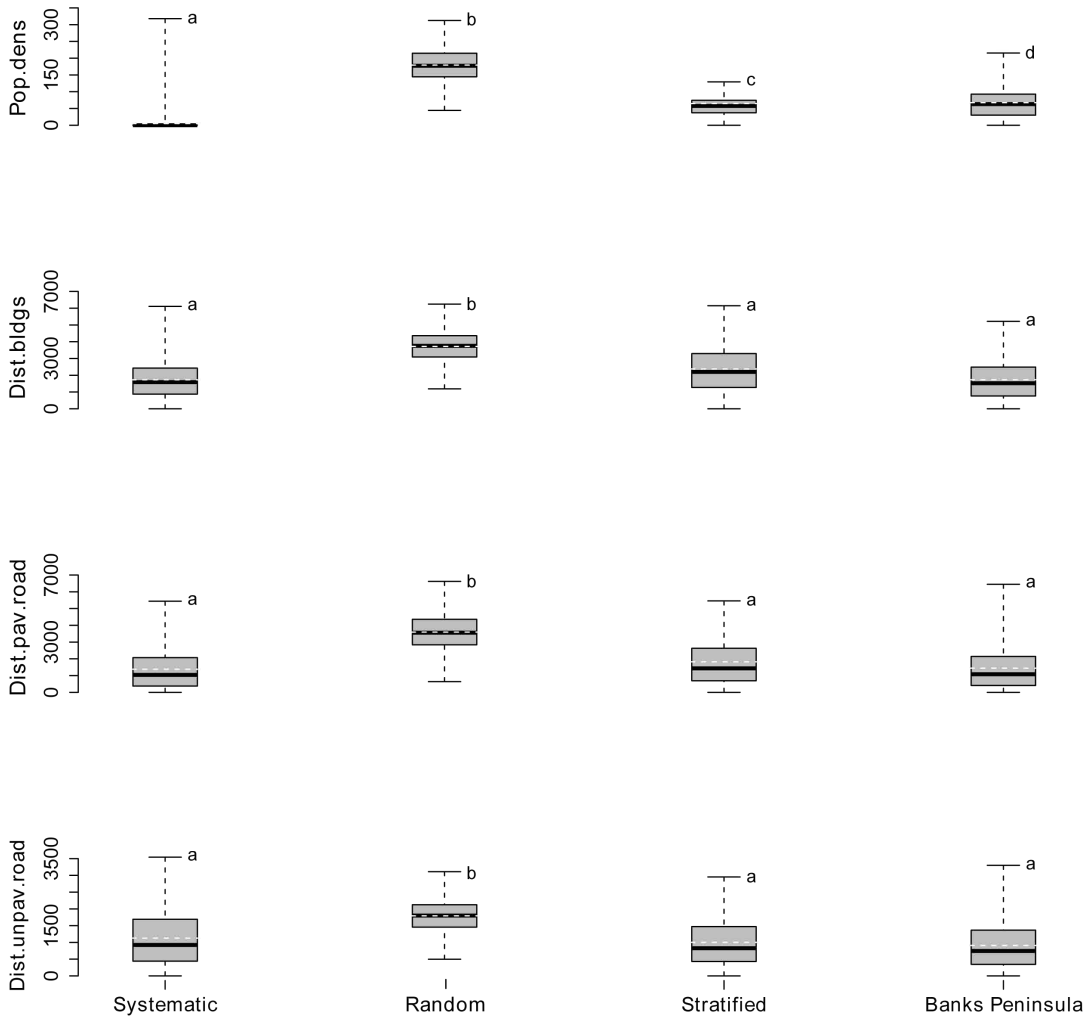

Figure 2.4. Box and whisker plots showing variation around the median of the human-related variables using three different survey methods. Solid black lines within grey box represent the median; dashed white lines the mean; whiskers represent the 10th and 90th percentiles. Different letters above the boxes indicate significant differences ($P < 0.001$) in the F-test and Wilcoxon test.

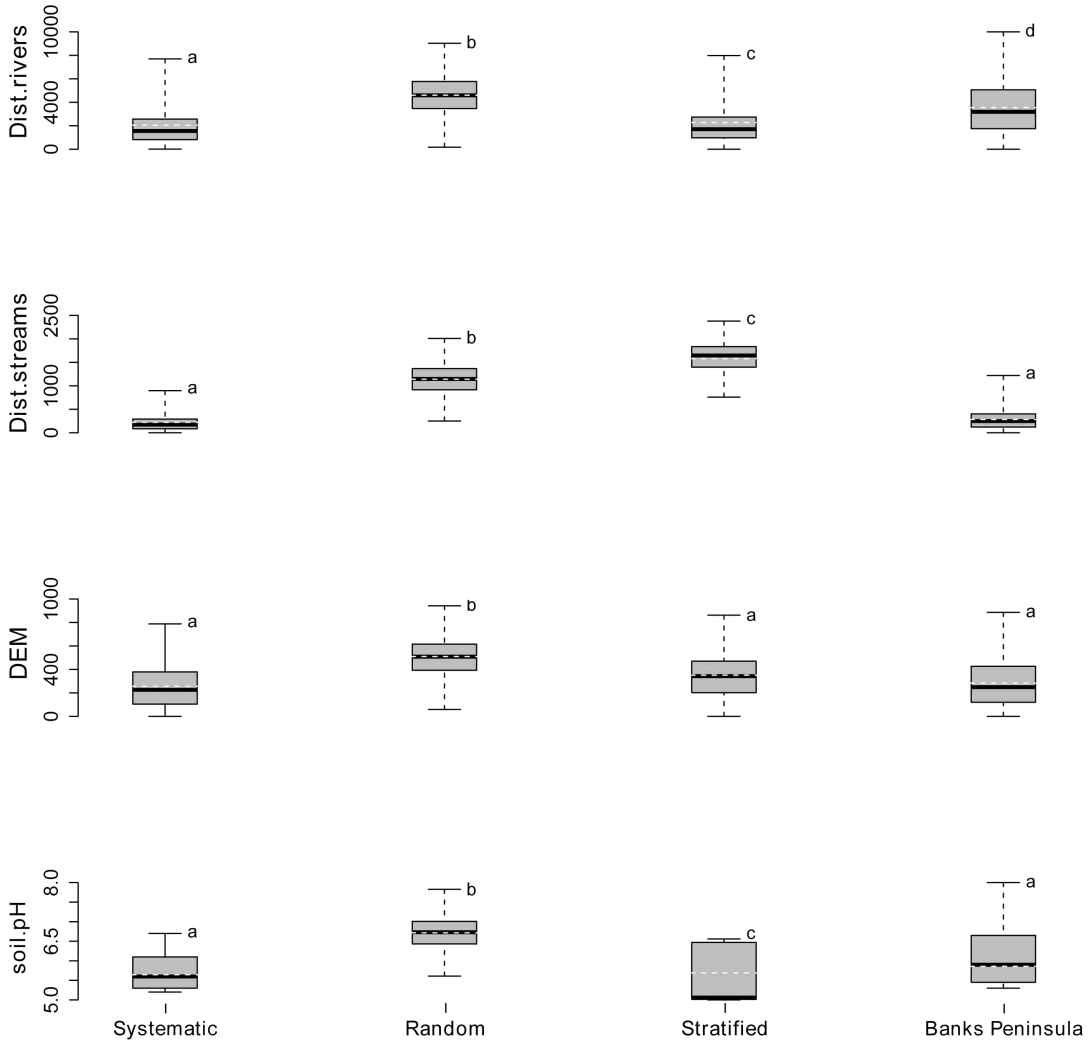

Figure 2.5. Box and whisker plots showing variation around the median of the environmental variables using three different survey methods. Solid black lines within grey box represent the median; dashed white lines the mean; whiskers represent the 10th and 90th percentiles. Different letters above the boxes indicate significant differences ($P < 0.001$) in the F-test and Wilcoxon test.

4); slope (4); for distance measures (17); and for soil pH (4). Once I checked that the raw data were not errors (i.e. reasonable observed values), I did not drop these outliers from further analysis as potentially useful information might be lost.

For the test of normality, the results from Lilliefors (Kolmogorov-Smirnov) test demonstrated that the data came from non-normal distributions (P-values < 0.001 for all the explanatory variables). Thus (see Chapter 4), I transformed selected explanatory variables into log 10 [x] + 1 to yield approximately normal distributions and to deal with zero value terms. These transformations also enhance the linear relationships (see Chapter 4) and are often needed with variables like distance measures (Zuur *et al.*, 2009).

For the multicolinearity test, a Spearman's rank correlation matrix highlighted that variables related to precipitation and moisture were strongly positively correlated ($rho > 0.80$, $P < 0.001$). The temperature-related variables were also strongly correlated ($rho > 0.60$, $P < 0.001$) but not with solar radiation. Elevation data was correlated with climate variables (e.g. $rho > 0.35$, $P < 0.001$) but not significantly with mean soil pH (Table 2.3 and Table 2.4). All human-related variables were also weakly correlated. The VIF analysis emphasized the magnitude of multicolinearity between precipitation-related and between temperature-related variables (Table 2.5) that have been found in the Spearman's correlation matrix. For further analysis of colinearity (see Chapter 3 and Chapter 4), I decided to use only those variables with VIFs ≤ 5.0 excluding aspect and slope already included in the calculation of solar radiation, so leaving a total of eleven variables (i.e. annual precipitation, growing degree days, solar radiation, population density and distance to buildings, distance to paved and unpaved roads, distance to permanent streams and rivers, elevation and mean soil pH; Appendix F). Further analysis on the latter dataset showed that the problems of colinearity were not met (e.g. $rho < 0.5$) with only elevation data correlated with GDD ($rho > 0.5$, $P < 0.001$). Therefore, elevation was not used in some of the analyses in this thesis (see Chapter 4).

Table 2.3. Spearman's rank correlation (*rho*) matrix between the continuous explanatory variables that have been detected by the systematic sampling approach (d.f. 1227). The statistical significance of correlations ($P < 0.001$) is shown in bold. This figure is divided into parts (on next page...)

	P.tot	P.sum	P.win	Av.temp	Min.temp	Max.temp	GDD	Evap.tot	Moist.ind	Sol.rad
P.sum	**0.89**									
P.win	**0.93**	**0.82**								
Av.temp	**-0.44**	**-0.47**	**-0.47**							
Min.temp	**-0.10**	**-0.23**	**-0.27**	**0.81**						
Max.temp	**-0.50**	**-0.47**	**-0.43**	**0.90**	**0.52**					
GDD	**-0.51**	**-0.50**	**-0.53**	**0.99**	**0.77**	**0.90**				
Evap.tot	**-0.52**	**-0.49**	**-0.53**	**0.98**	**0.72**	**0.94**	**0.99**			
Moist.ind	**0.68**	**0.68**	**0.69**	**-0.52**	**-0.36**	**-0.46**	**-0.55**	**-0.54**		
Sol.rad	0.01	0.01	-0.01	-0.01	0.02	-0.05	-0.01	-0.02	**-0.61**	
Pop.dens	**-0.23**	**-0.23**	**-0.22**	**0.27**	**0.16**	**0.22**	**0.29**	**0.26**	**-0.20**	0.02
Dist.bldgs	**0.20**	**0.19**	**0.21**	**-0.47**	**-0.35**	**-0.44**	**-0.49**	**-0.49**	**0.24**	-0.03
Dist.pav.road	0.09	0.05	0.07	**-0.24**	**-0.12**	**-0.25**	**-0.27**	**-0.27**	**0.12**	-0.06
Dist.unpav.road	**-0.12**	-0.01	**-0.14**	-0.07	**-0.10**	-0.07	-0.02	-0.02	**-0.10**	0.04
Dist.rivers	**-0.41**	**-0.46**	**-0.38**	-0.05	-0.07	**-0.10**	-0.03	-0.07	**-0.30**	0.02
Dist.streams	**-0.15**	**-0.15**	**-0.17**	**0.17**	**0.11**	**0.15**	**0.18**	**0.18**	**-0.17**	0.04
DEM	**0.43**	**0.42**	**0.42**	**-0.89**	**-0.61**	**-0.90**	**-0.89**	**-0.91**	**0.49**	-0.03
Aspect	-0.08	-0.01	-0.07	-0.04	-0.06	-0.02	-0.02	-0.02	-0.06	0.08
Slope	**0.14**	**0.11**	**0.14**	**-0.24**	**-0.13**	**-0.27**	**-0.25**	**-0.27**	**0.16**	-0.06
Soil.pH	0.02	0.05	0.04	**-0.26**	**-0.28**	**-0.22**	**-0.24**	**-0.23**	**0.11**	-0.02

Table 2.4. . . . continued from previous page

	Pop.dens	Dist.bldgs	Dist.pav.road	Dist.unpav.road	Dist.rivers	Dist.streams	DEM	Aspect	Slope
Dist.bldgs	**-0.35**								
Dist.pav.road	**-0.30**	**0.59**							
Dist.unpav.road	-0.03	**0.18**	0.04						
Dist.rivers	**0.14**	**0.16**	**0.15**	**0.22**					
Dist.streams	**0.11**	-0.08	-0.06	0.04	0.06				
DEM	**-0.24**	**0.47**	**0.29**	0.07	**0.15**	-0.02			
Aspect	0.00	0.02	0.05	0.05	0.07	0.03	0.04		
Slope	**-0.12**	**0.19**	**0.22**	0.03	**0.14**	0.04	**0.27**	**0.11**	
Soil.pH	-0.05	**0.13**	0.03	0.08	0.08	0.00	**0.20**	-0.04	**0.23**

Table 2.5. Variance inflation factors (VIF) of all the continuous explanatory variables calculated in the 1227 points of the systematic sampling method.

	VIF
P.tot	5.1
P.sum	26.81
P.win	32.62
Av.temp	1625
Min.temp	180.81
Max.temp	335.12
GDD	2.93
Evap.tot	264.64
Moist.ind	110.21
Sol.rad	2.64
Pop.dens	1.91
Dist.bldgs	2.72
Dist.pav.road	1.73
Dist.unpav.road	1.22
Dist.rivers	1.82
Dist.streams	1.13
DEM	2.83
Aspect	1.41
Slope	1.71
Soil.pH	1.23

For the spatial autocorrelation, the results from Moran's I test indicated that there was a significant trace of spatial autocorrelation between all the explanatory variables ($P < 0.001$; Table 2.6). All variables were strongly correlated over space, but at different distances (Appendix G). The climate variables showed positive autocorrelations over the shortest distances and three out of four human-related variables, as well as environmental variables, showed positive autocorrelations at short and intermediate distances. As the distance continues to increase, all of the climate and human-related variables, with some exceptions for environmental variables, exhibited no significant autocorrelations at the greatest distance. Thus, I applied linear models to deal with spatial autocorrelation of residuals (see Chapter 4).

Table 2.6. Summary results of spatial autocorrelation for the continuous explanatory variables extracted for the 1227 points from the systematic sampling approach. The columns indicate: *I* the observed value of Moran's *I*; *E(I)* the expectation for the mean-centred cases; *Var(I)* the variance of the statistic under randomization; Standard deviate of Moran's *I*; *P*-value of the test for the alternative that $I > E(I)$.

	I	*E(I)*	*Var(I)*	St.deviate	*P*-value
P.tot	0.98	-0.0008	0.0014	26.06	< 0.001
P.sum	0.97	-0.0008	0.0014	25.83	< 0.001
P.win	0.98	-0.0008	0.0014	26.13	< 0.001
Av.temp	0.81	-0.0008	0.0014	21.49	< 0.001
Min.temp	0.89	-0.0008	0.0014	23.78	< 0.001
Max.temp	0.81	-0.0008	0.0014	21.64	< 0.001
GDD	0.82	-0.0008	0.0014	21.7	< 0.001
Evap.tot	0.81	-0.0008	0.0014	21.67	< 0.001
Moist.ind	0.48	-0.0008	0.0014	12.84	< 0.001
Sol.rad	0.07	-0.0008	0.0014	1.95	< 0.05
Pop.dens	0.37	-0.0008	0.0013	10.11	< 0.001
Dist.bldgs	0.87	-0.0008	0.0014	23.17	< 0.001
Dist.pav.road	0.89	-0.0008	0.0014	23.56	< 0.001
Dist.unpav.road	0.82	-0.0008	0.0014	21.36	< 0.001
Dist.rivers	0.94	-0.0008	0.0014	25.24	< 0.001
Dist.streams	0.32	-0.0008	0.0013	8.48	< 0.001
DEM	0.7	-0.0008	0.0014	18.54	< 0.001
Aspect	0.08	-0.0008	0.0014	2.23	< 0.05
Slope	0.15	-0.0008	0.0014	4.09	< 0.001
Soil.pH	0.41	-0.0008	0.0014	10.92	< 0.001

2.5 Discussion

The first goal of this chapter was to identify which available GIS data layers may best describe this highly variable landscape in the context of studying the spatial distribution of (native or alien) plant species. The results of automated workflows as a linear sequence of GIS operations and tools (i.e. Geoprocessing and Spatial Analysis) generated relevant GIS data layers that have been stored in a geodatabase of Banks Peninsula. Geoprocessing is useful because it is repeatable and self-documenting. If it is integrated with spatial analysis (so-called geospatial analysis) as iterative processes or methods of modelling it may generate results and evaluate them at the same time. To enhance the results in order to obtain the best representation not only of heterogeneous environment, there is a clear need for the combined use of GIS, remote sensing, spatial analysis and expert knowledge. Further development of the interoperability between GIS and RS data and tools associated with spatial analysis would be a valuable technique in the study of plant species distribution not only in a highly variable landscape such as Banks Peninsula.

In my study, although the available data layers that best described the Peninsula environments have been identified, there is room for further improvement. For instance, the layers used as surrogates for human-related impact, for example, human population density, distance to buildings, distance to paved and unpaved roads, may be inadequate. The 1983-1988 systematic survey had for example sampled the Peninsula environments with some sampling limitations (e.g. detecting fewer population density areas and in areas near rivers). Land-use history was also inferred from the data rather than assessed independently (see Methods). The arguments about the importance of land-use and -management would be much stronger if an independent assessment of land-use and land-cover will be made. Another limitation can be seen in the fact that Hugh Wilson's plots were established before the days of GPS units, resulting in an error of $\pm$100 m of their spatial position (Susan Wiser personal communication). This means that the intersections with spatial layers need to accommodate this error. However, moving in all the directions for 100 m would have not changed the estimates of the data layers (i.e. explanatory variables) as they had a coarse spatial resolution (i.e. 500 $\times$ 500 m) but excluding DEM layer of 10 $\times$ 10 m spatial resolution. The derived measures from elevation, such as aspect and slope, have been assessed directly on each plot by Hugh Wilson and this may have been given the best estimate for these explanatory variables.

In my case, once these available data have been identified and quantified the second goal was to test if the Banks Peninsula systematic sampling survey that contains the species data is good enough to detect the range of environments found on the Peninsula. Although the systematic and random sampling methods are purely spatial techniques and extra information about the environments is needed *a priori* to conduct a stratified sampling survey, the results indicated that the systematic sampling survey is the most accurate method, followed by the stratified and random methods. Thus, consistent with the findings of Hirzel and Guisan (2002) and Roleček *et al.* (2007), the first two methods (i.e. systematic and stratified sampling) performed well confirming the validity of those approaches when dealing with a heterogeneous landscape such as Banks Peninsula characterized by highly variable climatic, human-related and environmental factors.

Obviously, a range of different sampling methods rather than these unbiased sampling designs (e.g. grid, random points and stratified targeted) can be used [see Hirzel and Guisan (2002); Rew *et al.* (2006); Maxwell *et al.* (2012)]. For instance, to detect species presence/absence and abundance in early stage of plant invasions, random transects and roadside sampling methods can be used. However, "because of the fragmented distribution of the plant species and to best perform, these methods need to increase the number of samples, leading into more time to detect and into less efficiency" (Morrison *et al.*, 2008). When plant species populations are patchier and dispersed, like alien plant species at early and later stages of invasion, the adaptive cluster sampling methods are generally proved to be the most time-efficient and effective in detecting plant species (Thompson, 2006). However, the use of adaptive cluster sampling methods has only been recently discovered for surveying alien plant species and it requires good computational effort. In conclusion, we need to keep in mind which sampling methods best achieve the objectives/goals of our study (Maxwell *et al.*, 2012).

Although the systematic survey performed better than the other methods, the latter detected fewer population density areas and was conducted near rivers. This may indicate that the 1983-1988 systematic survey was carried out in less urbanized areas and in areas more freely accessible by chance or because areas with high population density are rare on the landscape. As sampling is a money and time consuming task, prioritisation of requirements is of great importance (Hirzel and Guisan, 2002). In this sense, I confirm the findings of Rew *et al.* (2006) and Hirzel and Guisan (2002) that although there may be limitations to the systematic sampling method [e.g. the length of time required, up to 5 years; a restricted choice of

plot selection *sensu* Hirzel and Guisan (2002)], or it may be adequate for sampling grassland vegetation in New Zealand (Wiser and Rose, 1997; Hurst and Allen, 2007) but undersampling in forest and probably in sand dunes and cliffs (Phil Hulme personal communication), this is the "best" design option when the aims are to: (1) conduct a comprehensive floristic survey over a heterogeneous landscape such as Banks Peninsula, and (2) model within it the distribution of native or alien plant species in relation to the spatial distribution of environmental factors (c.f. Huebner, 2007; Roleček *et al.*, 2007).

Once the "best" sampling method has been identified, the third goal was to determine if the data used as explanatory variables to describe plant species distribution violated any statistical assumptions. The results show that a series of problems (i.e. outliers, colinearity, non-normality and spatial autocorrelation) were encountered and these may seriously affect the results of an analysis. In all cases, the problems can lead to statistical models that are wrong (Kühn and Dormann, 2012). Zuur *et al.* (2010) suggested that such problems can be avoided only by applying systematic data exploration before embarking on analysis. In the Banks Peninsula geodatabase for example, the results have shown that the data layers are either spatially autocorrelated or suffer different degrees of colinearity. Nevertheless, the spatial autocorrelation of those potential variables that varied over distance could potentially reveal the effects of underlying ecological and environmental gradients (Guo *et al.*, 2012). Thus, it was crucial to build a spatial component into the statistical models for a better understanding of the pattern of species on the Peninsula and to increase confidence in data interpretation (see Chapter 4). If spatial autocorrelation is ignored or removed from among the explanatory variables this would also remove most of the power of the explanatory variables (Guo *et al.*, 2012), and we simply would not know if the results are to be trusted. As already stated by Diniz *et al.* (2003), the presence of residual spatial autocorrelation should always be tested for in spatial ecology and appropriate methods should be used if there is shown to be significant spatial autocorrelation (Kühn and Klotz, 2007). Colinearity is another statistical challenge, as it could affect the response variable interactively. On the one hand, if strong colinearity is detected, an easy way to deal with it could be not to include highly correlated variables in the analysis. However, information and understanding may be lost when ecological patterns and processes are influenced by additional factors not selected. On the other hand, adding more variables potentially offers more hypotheses and tests, and interpretations of greater explanatory power (Guo *et al.*, 2012). Thus, a trade off in selecting variables is always necessary. With these issues adequately addressed in

a way that makes ecological sense, questions asked of the dataset, regarding plant species patterns and processes will not be biased by the quality of the data and the chances of making wrong ecological conclusions and poor recommendations will be reduced.

Chapter 3

Environmental and human-related factors along elevational gradients underlying native and alien plant communities structure and patterns

"Focusing on how alien patterns vary along directional natural gradients with strong human driven propagule pressure is a promising research area in invasion ecology." (Marta Carboni)

3.1 Abstract

In my study, dominant gradients in native and alien vegetation patterns and the environmental factors that underlie these were assessed along environmental gradients in a heterogeneous and disturbed landscape of Banks Peninsula. A floristic survey of over 1200 systematically located 6 × 6 m plots, together with climate, human-related and environmental data were used. Both ordination and classification techniques were employed to illustrate changes in vegetation composition and environmental heterogeneity across the Peninsula. These techniques were integrated with analyses of the differences in native and alien species distribution and how these affect community structure. The analyses of rank occupancy, elevational range, homogenization effects and nestedness within or between native and alien dominated plots, and within or between separate elevational bands, indicated that the native and alien species communities were spatially and ecologically segregated due to different responses to the human land-use gradient (i.e. land-use history and management) *in primis*, and to the climate and environmental factors *in secundis*, principally along an elevational gradient. Human-land use factors appear most strongly linked to the distribution of alien species and lead to increased homogenization of the native community. In addition, the results indicated that variation in abiotic conditions might explain greater dissimilarity and nestedness within native communities besides the presence of low levels of propagule pressure. Thus, the role played by contemporary and historical human impacts cannot be ignored and, even along a marked environmental gradient, it remains the main determinant of native and alien species structure and patterns. My results also demonstrated that where the recipient site is more disturbed biotic homogenization is stronger. This indicates that biotic homogenization is a more serious problem for highly managed than for less managed areas.

Keywords: Biological invasions, biotic homogenization, disturbance, exotic species, nestedness, dissimilarity.

3.2 Introduction

Understanding how and why native and alien plant species distribution and community structure differ along environmental gradients with associated human-related factors (e.g. land-use history and management and related propagule pressure, *sensu* Lockwood *et al.*, 2005) is a promising research area in the field of invasion ecology (Marini *et al.*, 2009; Carboni *et al.*, 2011; Marini *et al.*, 2012). Across a landscape, native and alien species distribution patterns can be influenced by a number of abiotic (e.g. climate, topography and soil fertility) and biotic factors (e.g. water, nutrients or livestock grazing; Pettit *et al.*, 1995; Richardson *et al.*, 2000; Pyšek *et al.*, 2002; Arévalo *et al.*, 2005; Prober and Wiehl, 2012). Human-related disturbances such as urbanization (Oneal and Rotenberry, 2008) or land-use history (e.g. forest clearance; Brown and Boutin, 2009) have been shown to be dominant factors affecting both native and alien species richness [(Hobbs and Huenneke, 1992), see Chapter 4] and to determine changes in plant species community structure either as an impact of disturbance or a systems recover (Wiser *et al.*, 1998). Moreover, native and alien communities are spatially segregated along gradients of human-related activities (Cilliers and Bredenkamp, 2000; Kelly *et al.*, 2009; Mosher *et al.*, 2009; Otýpková *et al.*, 2011). Bearing in mind this, if we are to fully understand the major patterns in the composition of native and alien vegetation and the related environmental gradients in a heterogeneous landscape, we must consider the role of contemporary and historical land-use and -management, especially where these human-related disturbances covaries with climate and environmental gradients (Brown and Boutin, 2009; Parker *et al.*, 2010; Boughton *et al.*, 2011; Marini *et al.*, 2012) and see Chapter 4.

Where the land-use gradient is linked to past/recent management in heavily modified landscapes, it is an important driver of native and alien species distribution (Vitousek *et al.*, 1996; Fornwalt *et al.*, 2003) and see Chapter 4. This may promote the establishment of alien species via increased colonization pressure *sensu* Lockwood *et al.* (2009). The spread of generalist cosmopolitan alien species may certainly change diversity and the community structure, diminishing, for example, dissimilarity in species composition between sites (e.g. increasing biotic homogenization due to replacement of native species; McKinney and Lockwood, 1999; Olden and Poff, 2003) but the spread of alien species may also lead to an increase of dissimilarity either due to the plot size/grain and the extent to which the compared regions are invaded with less dissimilarity at small grain and extent and greater dissimilarity at large grain and extent (Pyšek and Richardson, 2006).

Patterns of native and alien plant communities have also been shown to be separated along elevational gradients, where native species may be found in higher elevation sites than alien species (Cantero *et al.*, 2003; Wiser and Buxton, 2009; Conn *et al.*, 2011). Along this gradient, increased distinctiveness (i.e. dissimilarity) within/between communities may also be found and it may occur for several reasons. Different alien species, for instance, may establish in different and suitable habitats within their potential distribution/elevational range (Becker *et al.*, 2005; Pauchard *et al.*, 2009; Haider *et al.*, 2010; Alexander *et al.*, 2011) but invasions are not always accompanied by extinction of native species and these extinctions may be only of small/local extent (Lososová *et al.*, 2012). Another reason is the fact that, more specialized native species may drive dissimilarity along elevational gradients since these communities are often structured by elevation while generalist alien species with broader environmental tolerances may be more similar across the elevational range where they are found (Seipel *et al.*, 2012). Furthermore, in human modified habitats (e.g. urban areas especially at low- to mid-elevation) there is an ever-increasing number of alien species in the vegetation (Cilliers and Bredenkamp, 2000) where the number of alien species sustained may differ considerably (Cantero *et al.*, 2003) from those in less modified areas (Chytrý *et al.*, 2008a; Gassó *et al.*, 2012). It is possible that these will also differ in the degree of dissimilarity in the overall species composition (i.e. biotic homogenization) associated with invasions (c.f. Oneal and Rotenberry, 2008).

In addition, propagule pressure and colonization (i.e. naturalization), environmental tolerances, and susceptibility to human disturbance may all alter the communities' structure, leading, for example, to nested distributions (Patterson, 1990; Lomolino, 1996; Worthen *et al.*, 1998; Bruun and Moen, 2003) where the alien species may be more nested than native species (Foxcroft *et al.*, 2007; Vilá *et al.*, 2009a; Baeten *et al.*, 2012). Nestedness occurs when assemblages in species-poor sites are composed of species that constitute subsets of species occurring in successively richer sites (Wright and Reeves, 1992) or when tolerance to abiotic factors is the major driver for the occurrence of nestedness in the communities (Atmar and Patterson, 1993; Lomolino, 1996; Wright *et al.*, 1998; Almeida-Neto *et al.*, 2008). Likewise, Occupancy Frequency Distribution (i.e. distributions of the numbers of species occupying different numbers of areas, namely OFD; McGeoch and Gaston, 2002; Jenkins, 2011) and Rank Occupancy Rate (i.e. the rate of change in occupancy, namely ROR; Jenkins, 2011) may be used to explain how native and alien species respond to disturbance through time and space, where alien species may colonize

faster and a greater number of habitats than native species because these are more adapted to human-related disturbance (Fox and Fox, 1986; Rose and Hermanutz, 2004).

There is an emerging consensus that biotic homogenization and nestedness depends on the spatial and temporal scales (McKinney and Lockwood, 1999; Olden *et al.*, 2004; Pyšek and Richardson, 2006; Chen *et al.*, 2010), where species composition and structure may vary over time and at different scales. Nevertheless, there is still little or no understanding of the vegetation distribution patterns (i.e. composition and structure) controlled by contemporary and historical land-use and -management in particular along elevational gradients. This is the focus of the present chapter.

I have used here data from the 1983-1988 Banks Peninsula floristic survey to address the following questions:

1. Does invasion lead to distinct native and alien plant communities?
2. Do native and alien dominated communities segregate along abiotic (i.e. climate) or biotic gradients (i.e. land-use history and management)?
3. How do alien species influence levels of homogenization and community dissimilarity within and across different plant communities?
4. How do the different environmental tolerances of native and alien species shape community structure and nestedness?

3.3 Materials & Methods

3.3.1 Study area

The Banks Peninsula study area is described in Chapter 2.

3.3.2 Floristic data

The comprehensive floristic survey conducted between 1983 and 1988 over the entire Banks Peninsula is described in Chapter 2. For the analyses here, I transformed the relative abundance of native and alien species in the plot into its arbitrary and continuous percentage values (i.e. 0-100%) using the function *vegtrans* contained in the *labdsv* package (Roberts, 2012).

3.3.3 Explanatory variables

The values of 11 climate, environmental and human-related variables derived are described in Chapter 2.

3.3.4 Statistical analysis

3.3.4.1 Plant species composition patterns and processes

To identify the dominant gradients in the native and alien plant community composition and the environmental factors that underlie these on Banks Peninsula, I used the Non-Metric Multidimensional Scaling technique (NMDS; Kruskal, 1964) contained in the *vegan* package (2.1-14; Oksanen *et al.*, 2012) - a robust method of unconstrained ordination (Minchin, 1987; Oksanen *et al.*, 2012; Roberts, 2012) to ordinate plots in "plant space" (Parker *et al.*, 2010). Because datasets that are non-parametric (i.e. data that are non-normally distributed and have a large proportion of zero values) can be reliably analysed using this technique (Parendes and Jones, 2000; Hochstedler *et al.*, 2007) and because any depiction is based on maximizing the rank correlation between the calculated similarity/dissimilarity distances and the plotted distances (*sensu* Kruskal, 1964), rather than numerical distances, NMDS is less susceptible than other ordination methods to outlying responses to underlying gradients (Fasham, 1977; Kenkel and Orlóci, 1986; Clarke, 1993; Hochstedler *et al.*, 2007; Parker *et al.*, 2010). Moreover, the NMDS technique graphically depicts similarity and/or dissimilarity within or between the assemblages of vegetation communities. Similarity/dissimilarity indices have proven to be a useful method for comparing species composition between plots (i.e. beta diversity; Parendes and Jones, 2000; Wearne and Morgan, 2004; Chao, 2005; Lososová *et al.*, 2012). To do so, I firstly selected the most suitable distance matrix (Faith *et al.*, 1987) after comparing different dissimilarity indices (e.g. Canberra, Jaccard and Bray-Curtis) that provided the strongest relationship in the rank orders of correlations with the scaled Banks Peninsula environmental gradients (Oksanen *et al.*, 2012). Based on the highest values of the dissimilarity indices (i.e. high rank-order dissimilarity with gradient separation), I decided to use the Jaccard dissimilarity index (Jaccard, 1901) based on species abundance at each plot (Chao *et al.*, 2006), although, similar rank-order values were found using this index based on species presence-absence. The Jaccard index is metric and ranges between 0 and 1, where a result of 1 means that the two assemblages have no species in common (completely dissimilar), and a result of 0

means that the assemblages are similar (identical samples). I then used the *metaMDS* function (Oksanen *et al.*, 2012) that selects the model with the lowest stress or the best model fit. Once the number of dimensions has been specified, the *metaMDS* function finds a stable solution for the NMDS by using several random starts (i.e. iteration, in this case $n = 100$) and comparing the lowest stress index with the initial model to see if the stress is lower. The *metaMDS* function standardises the scaling in the result using *postMDS* function.

I then tested the significance of the NMDS ordination of plots along the axes using multivariate analysis of variance (MANOVA) with the Pillai-Bartlett test statistic following Zechmeister *et al.* (2007). To test which of the environmental factors (i.e. explanatory variables) are related to the variation in Banks Peninsula plant community patterns, I used the *envfit* function with 10000 permutations and then fitted vectors were overlaid onto the ordination. After that, I classified the vegetation from 1227 plots into classes (i.e. types) using a dendrogram to plot hierarchical clustering. For a better representation of the dendrogram, I used the average distance between cluster centroids (i.e. average linkage method *sensu* UPGMA; Oksanen *et al.*, 2012).

To optimize the classification for a given number of clusters (i.e. number of classes) I used *K*-means clustering with 100 iterations and random starts, optimized with Hellinger transformation as standardizations (i.e. square root of data divided by plot totals; Legendre and Gallagher, 2001). I then tested the *K*-means clustering output to determine if the given number of clusters is the optimal number (Oksanen, 2012). The resulting classes have been added "manually" to the ordination graph. To assess the strength and significance of the association between species and clusters, I used the *multipatt* function in the *indicspecies* package (De-Caceres and Legendre, 2009). This function studies the combinations of the input clusters and compares each combination with the species matrix to identify indicator species (i.e. indicator values; Dufrêne and Legendre, 1997).

In order to identify the abiotic and biotic factors associated with the plant community types, I quantified: the mean number of native and alien species, the alien to native species richness ratio (ANR), the native and alien species richness relationship using Spearman's rank correlation coefficient (*rho*), the proportion of plots dominated by alien species; the dominant native and/or alien species with the total number of plots occupied, and the mean of the key climate, environmental and human-related variables. For each of the community types, I also estimated mean Occupancy Frequency Distribution, mean dissimilarity index values, homogeniza-

tion effect and nestedness (see below). Within each of the community types, Rank Occupancy Rate (see below) was tested but as no pattern was discerned it was not included in the results.

3.3.4.2 Plant species distribution and structure

To examine the distribution of plant communities across all Banks Peninsula environmental gradients and the processes affecting the community composition and structure, I estimated for native and alien species separately: (i) the Occupancy Frequency Distribution and the Rank Occupancy Rate; (ii) the elevational ranges and the nestedness. Given the large elevational range on Banks Peninsula, I also calculated: the dissimilarity index values, homogenization effect and nestedness of native and alien species dominated communities for plots within each of five elevational bands (see below).

For the Occupancy Frequency Distribution (OFD; McGeoch and Gaston, 2002), I calculated the absolute occurrence (i.e. number of occupied plots) of each native and alien species separately. I then used a Rank Occupancy Rate (ROR) separately for each native and alien species to test if there may be a trend in the species occupancy frequency with alien species more widespread than native species due to their adaptation to human-related disturbances. This measure is calculated by separately ranking, from higher to lower values, the number of plots occupied by each of the native and alien species and dividing them by their respective maximum number of occupied plots.

To examine if there was a decrease of dissimilarity within native and alien dominated vegetation communities along the elevational gradient (0-920 m a.s.l.; see also Chapter 4) encompassed by Banks Peninsula, I calculated the mean of pairwise Jaccard dissimilarity index values of native and alien species communities separately for plots within each of five elevational bands (0 - 100, 101 - 200, 201 - 300, 301 - 400 and $>$ 400 m a.s.l.) chosen to ensure that each band had an approximately equal number of plots. I also used a *simper* function (Clarke, 1993) to perform pairwise comparisons of groups of plots to identify the average contribution of each native and alien plant species to the average overall similarity/dissimilarity index within native/alien dominated communities, and separately within each elevational band. The average contribution to dissimilarity means that the function displays the most important species for each pair of groups. These species contribute at least to 70% of the differences between groups. The species which consistently contribute

greatly to the average dissimilarity between groups are considered characteristic of the habitat/community type. Stratifying plots by elevational bands allowed me to examine the potential homogenization of community composition while controlling for the variation of key variables (e.g. climate; Hanspach *et al.*, 2008; Marini *et al.*, 2009, 2012). This approach is the first attempt to compare the degree of biotic homogenization across habitat types with different regimes and intensity of disturbances along elevational gradients. Within each elevational band, I tested if pairs of assemblages had been homogenized or differentiated due to the introduction of alien species using the homogenization index H (Rahel, 2000).

$$H = Jtotal - Jnative,$$

where $Jtotal$ is the pairwise Jaccard similarity/dissimilarity between all species and $Jnative$ is that between native species only. H ranges from -1 to 1. Positive values indicate that dissimilarity of native species is lower than dissimilarity of all species, therefore alien species contribute to differentiation. Negative H index values indicate that the introduction of alien species contributes to the homogenization of species assemblages (McKinney, 2004; Lososová *et al.*, 2012).

Given the large elevational range on Banks Peninsula and the covariance of human-related disturbances with elevation (i.e. land-use history and management; Wiser and Buxton, 2008, 2009) and Chapter 4, I performed a nested subset analysis to detect non-random patterns of the native and alien community separately (Patterson, 1990; Worthen and Rohde, 1996; Wright *et al.*, 1998; Honnay *et al.*, 1999). Nestedness occurs when species are distributed non-randomly with respect to a common set of extrinsic variables (Atmar and Patterson, 1993; Lomolino, 1996; Wright *et al.*, 1998; Almeida-Neto *et al.*, 2008). When species respond differently to the major drivers/gradients related to species presence/abundance (e.g. disturbance), the community as a whole will not be nested (Driscoll, 2008). In contrast, when species respond similarly to environmental gradients (e.g. soil conditions or disturbance), communities will be nested (Elmendorf and Harrison, 2009). To test this, I calculated the Nestedness metric based on Overlap and Decreasing Fill (NODF; Almeida-Neto *et al.*, 2008) contained in the *vegan* package (Oksanen *et al.*, 2012). Nestedness is usually represented and calculated using binary data (i.e. presence-absence) matrices. According to Almeida-Neto *et al.* (2008), two basic properties are required for a matrix to maximize the degree of nestedness: complete overlap of the presences (i.e. 1's) in less-filled columns and rows (so-called Overlap) and (2) decreasing marginal totals (i.e. fills) between all pairs of columns and all pairs of

rows (so-called Decreasing Fill). The measure of nestedness for the whole matrix is given by these two properties (for further details see Almeida-Neto *et al.*, 2008). For both native and alien communities, I produced two species-plot matrices, with species either present as recorded in the plots (maximally packed) or ordered by increasing elevation of the plot but within their elevational range. Tests of nestedness of plots were based on 1000 randomizations of the matrix using a null model that constrained species abundance within plots and keeping the total sum constant whilst randomizing the occurrence of species within plots. The computed *P*-value expresses the possibility of generating a matrix that is more ordered than the given data matrix. Nestedness is considered significant if species incidence is closer to the pattern described above than would be expected by chance. To better understand whether native and alien species dominated vegetation communities composition vary in their nestedness along the elevational gradient, I also performed this analysis within each of the five elevational bands.

3.4 Results

3.4.1 Plant species composition patterns and processes

NMDS attained a convergent two-dimensional solution with a stress of 4.8% (Shepard test, $R^2 = 0.99$), which can be interpreted as a "good" representation of the underlying data (Kruskal, 1964). On Banks Peninsula, the significant environmental factors that related to the native and alien community composition were the gradients of climatic-topographic factors (axis 2; Pillai $= 0.9$, $F = 3679$, $P < 0.001$) and human land-use and -management (axis 1; Pillai $= 2$, $F = 812$, $P < 0.05$; Figure 3.1).

Gradients of species arrayed from warmer and drier plots (typically at lower elevation) to cooler and wetter plots (typically at higher elevation) along axis 2 of the ordination. For example, alien species (e.g. *Lolium perenne*, *Dactylis glomerata*) are dominant at warmer sites with high solar radiation (drier north facing slopes), whereas native species (e.g. *Poa cita*, *Pteridium esculentum* and *Festuca novae-zelandiae*) are more abundant at cooler sites with low solar radiation (steeper, south facing slopes) and in areas further away from buildings. The dominant gradient (i.e. axis 1) underlying species composition can be interpreted as related to a legacy of land-use history and management, with a shift in vegetation structure from a higher proportion of grass species per plot ($R^2 = 0.6$, $P < 0.001$, Table 3.1; for example *Lolium perenne* and *Trifolium* spp. swards) with higher fast growing alien grass

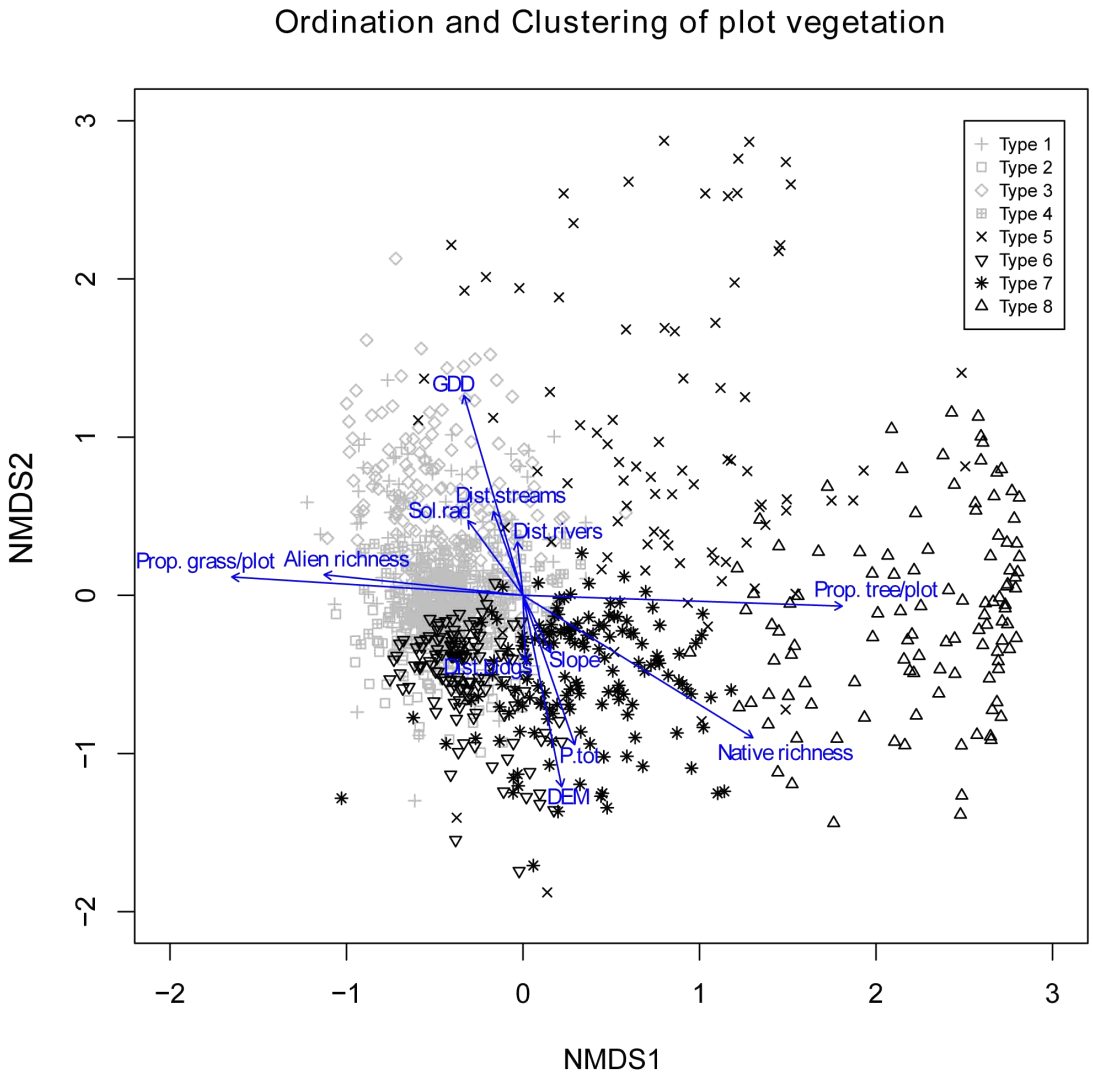

Figure 3.1. NMDS ordination of 1227 plots coded by the eight plant communities on Banks Peninsula. In ordination space, the dissimilar objects, in this case the Banks Peninsula species composition, are plotted far apart and the more similar objects are clustered in the ordination diagram. Vectors represent explanatory variables fitted on the NMDS ordination having P-values < 0.0001. Positions of plot scores and clusters are coded by a hierarchical clustering optimized by K-means clustering. Black or grey colours indicate if the cluster is dominated by native or alien species respectively.

species richness ($rho = 0.32$, $P < 0.001$) to less modified or regenerating areas with higher proportion of trees per plot ($R^2 = 0.72$, $P < 0.001$; for example *Melicytus ramiflorus* and *Fuchsia excorticata*) and higher native tree richness ($rho = 0.59$, $P < 0.001$; further details are given in Chapter 4).

The clustering analysis identified eight community types (Figure 3.1), full descriptions of which will be found in Appendix H. In summary, these community types ranked by invasion gradient (i.e. the proportion of plots dominated by alien species; Figure 3.2) and categorized by biotic factors are:

Type 1. Highly-modified lowland ($\bar{x} = 134 \pm 12.3$ m a.s.l.) pasture community on less steep slopes ($\bar{x} = 12.4^{\circ} \pm 0.76$) with 111 alien species present in 149 plots and indicator species such as *Taraxacum officinale*, *Lolium perenne* and *Trifolium repens*; 93% of this community is dominated by alien species such as *Lolium perenne*, *Dactylis glomerata* and *Anthoxanthum odoratum*

Type 2. Highly-modified rough pasture community with 211 alien species present in 266 plots at low- to mid-elevation ($\bar{x} = 263 \pm 9.6$ m a.s.l.) on less fertile soils. Alien species such as *Agrostis capillaris* and *Cynosurus cristatus* are the most common indicator species; 92% of plots falling in this community is dominated by alien species such as *Lolium perenne*, *Anthoxanthum odoratum* and *Dactylis glomerata*

Type 3. Drier-poor soil lowland ($\bar{x} = 156 \pm 10$ m a.s.l.) alien pasture community with indicator species such as *Rytidosperma racemosum* and *Trifolium glomeratum* with *Silene gallica*, particularly present close to roads; 66% of plots falling in this community is dominated by alien species such as *Lolium perenne*, *Anthoxanthum odoratum* and *Cynosurus cristatus*

Type 4. Lowland ($\bar{x} = 208 \pm 8.4$ m a.s.l.) alien grassland community on relatively steep slopes ($\bar{x} = 20.1^{\circ} \pm 0.6$) with 110 alien species present in 196 plots. *Trifolium* spp. and *Rytidosperma clavatum* are the most common indicator species; 59% of plots falling in this community is dominated by alien species such as *Lolium perenne* and *Anthoxanthum odoratum*

Type 5. Coastal ($\bar{x} = 160 \pm 16$ m a.s.l.) mixture of native and alien grasses and shrubs with indicator species such as *Scandia geniculata*, *Coprosma virescens* found in 87 plots particularly in the coastal perimeter and cliffs of the Peninsula; 44% of plots

falling in this community is dominated by alien species such as *Lolium perenne*, but also with native grass (*Poa cita*) and shrub (*Kunzea ericoides*)

Type 6. Mid-elevation ($\bar{x} = 302 \pm 17.2$ m a.s.l.) semi-native tussock grassland with 32 native grass species present and *Hydrocotyle novae-zeelandiae* var. *montana*, *Festuca novae-zelandiae* and *Poa cita* as indicator species; 43% of the plots belonging to this community is dominated by alien species such as *Lolium perenne*

Type 7. Mid-upland ($\bar{x} = 382 \pm 14.5$ m a.s.l.) on steep slopes ($\bar{x} = 23.3° \pm 0.67$) semi-native tussock grassland with indicator species such as *Pteridium esculentum*, *Digitalis purpurea* and *Hydrocotyle moschata* observed in 144 plots; 34% of this community is dominated by a pool of alien species such as *Rytidosperma clavatum*, *Anthoxanthum odoratum* and *Lolium perenne*

Type 8. Native second-growth forest and shrubland widely spread in 111 plots particularly in gullies ($\bar{x} = 442 \pm 15.7$ m a.s.l.) on steep slopes ($\bar{x} = 22° \pm 0.85$); 3% of this community is dominated by alien species. The majority of taxa are native shrub and tree species (36 and 28 species respectively) with *Melicytus ramiflorus* (most common indicator species; 11 dominated plots) and open environments dominated by *Poa cita* (25).

These community types encompass significant variation in plot composition (i.e. biotic factors) and conditions (i.e. abiotic factors) both within and between communities. The relative importance of factors such as GDD, annual precipitation, distance to buildings and slope, significantly characterized these community types. Full descriptions of these factors can be found in Appendix H.

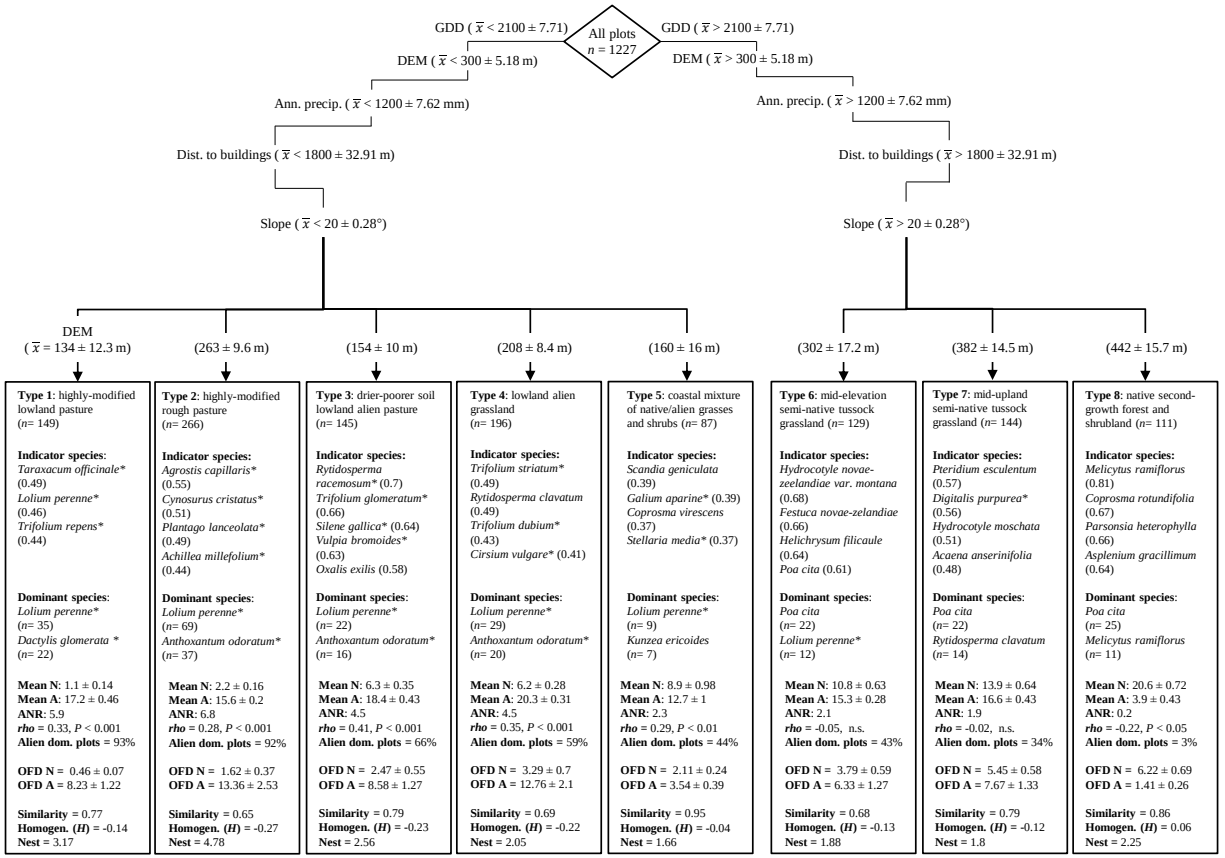

Figure 3.2. Hierarchical relationships of the abiotic and biotic factors associated with the community types (i.e. classes) recognized by the clustering analysis of plant communities on Banks Peninsula and overlaid onto the NMDS ordination. Shown here are mean ± SE of: GDD, elevation (DEM), annual precipitation (Ann. precip.), distance to buildings (Dist. to buildings) and slope characterizing the community types. Each community type is labelled with a short descriptive name. Species typifying community types are listed following an invasion gradient with scientific names and indicator values (square root of indicator values, see Methods). For each community types, the dominant species, the mean ± SE of native (N) and alien (A) species, the alien/native richness ratio (ANR), the Spearman's rank coefficient (*rho*) of native-alien species richness relationship, the dominated plots (%) by alien species, the mean ± SE of Occupancy Frequency Distribution (OFD) for native (N) and alien (A) species, the mean similarity, homogenization (*H*) and the nestedness (nest) are shown. The numbers of sample plots (n) are also shown. Alien species are indicated by *.

Table 3.1. Descriptive statistics of the explanatory variables fitted on the species community Non-Metric Multidimensional Scaling ordination (NMDS) and the coefficient of determination (R^2). *P*-values are based on permutation tests ($n = 10000$). Variables with $P < 0.0001$ are included as significant environmental vectors in Figure 3.1.

	Mean	Range	SD	R^2	*P*-values
Ptot	1239.61	640.41 - 1950.52	267.04	0.22	< 0.0001
GDD	2315.92	1537 - 2868	270.06	0.38	< 0.0001
Sol.rad	0.74	0.23 - 0.98	0.13	0.07	< 0.0001
Pop.dens	67.52	0 - 318	26.85	0.02	< 0.0001
Dist.bldgs	2970.61	0 - 7010	1152.71	0.04	< 0.0001
Dist.rivers	6697.82	1.31 - 9979	1814	0.03	< 0.0001
Dist.streams	261.93	0.32 - 2264	210.86	0.07	< 0.0001
DEM	256.11	0 - 797	181.38	0.35	< 0.0001
Slope	19.32	0 - 59.91	9.85	0.03	< 0.0001
Prop.tree	11%	0 - 100%	0.18	0.72	< 0.0001
Prop.grass	33%	0 - 100%	0.15	0.62	< 0.0001
Native richness	7.93	0 - 49	8.12	0.55	< 0.0001
Alien richness	16.34	0 - 44	6.56	0.29	< 0.0001

3.4.2 Plant species distribution and structure

The Occupancy Frequency Distribution showed that only a few alien species tend to occupy more plots than native species (*c.* 10 species found in more than 400 plots; Figure 3.3a). Of these, we find: *Dactylis glomerata* (956 occupied plots), *Trifolium repens* (947), *Lolium perenne* (940), *Holcus lanatus* (902), *Anthoxanthum odoratum* (867), *Crepis capillaris* (802), *Cynosurus cristatus* (736), *Cerastium fontanum* subsp. *vulgare* (676), *Trifolium dubium* (672). These few alien species (particularly pasture species) are widespread, while the rest (so-called satellite modes *sensu* McGeoch and Gaston, 2002) occupy relatively fewer plots ($\bar{x}alien = 30.5 \pm 9.6$). In contrast, the native species pool has few species that are widespread (*c.* 5 species found in more than 200 plots). Of these, we find: *Rytidosperma clavatum* (430 occupied plots), *Poa cita* (352), *Oxalis exilis* (292), *Wahlenbergia gracilis* (258), *Muehlenbeckia complexa* (208). The remaining native species tend to occupy a relatively high number of plots ($\bar{x}native = 60 \pm 2.6$) across Banks Peninsula. This is confirmed by the ROR that shows how alien species decrease more rapidly in plot occupancy than native species (Figure 3.3b). Within each of the community types (Figure 3.2), alien species tended to occupy more plots (*c.* 10.73 ± 1.35) when the community is dominated by alien

species (types 1-2-3-4) than in native dominated communities (*c.* 5.13 ± 1.9 plots; types 6-7-8).

Patterns emerged also in the native-alien species richness relationship analysis of each community types (Figure 3.2 and Appendix H). For communities that are dominated by alien species (types 1-2-3-4), there were significant positive relationships between native and alien species richness (*rho* between 0.28 and 0.41, $P < 0.001$ respectively; Figure 3.2). In contrast, the species richness relationship was slightly significantly negative only in one native dominated community (type 8; *rho* = -0.22, $P < 0.05$; Figure 3.2 and Appendix H).

The analysis of elevational ranges of the entire native and alien species pool showed that the 368 native species tended to occur at higher elevations ($\bar{x}native$ = 353 ± 10.3 m a.s.l.) than the 311 alien species ($\bar{x}alien$ = 162 ± 7.3 m a.s.l.; Wilcoxon rank sum test: W = 84818, $P < 0.001$). An additional analysis restricted to the 100 most abundant species confirmed that generalist alien species found at high elevations were those that also occurred at low elevations and those with the widest elevational ranges indicating broader environmental tolerances (e.g. *Lolium perenne*, *Dactylis glomerata*; Appendix I).

Analyses of the average Jaccard dissimilarity index across the entire elevational gradient and within each elevational band revealed that there was a consistent decrease in dissimilarity in the alien dominated communities ($\bar{x}Jalien = 0.73 \pm 0.01$), and this was lower than the consistent high level of dissimilarity in the native dominated communities ($\bar{x}Jnative = 0.93 \pm 0.01$, W = 59, $P < 0.001$; Figure 3.4).

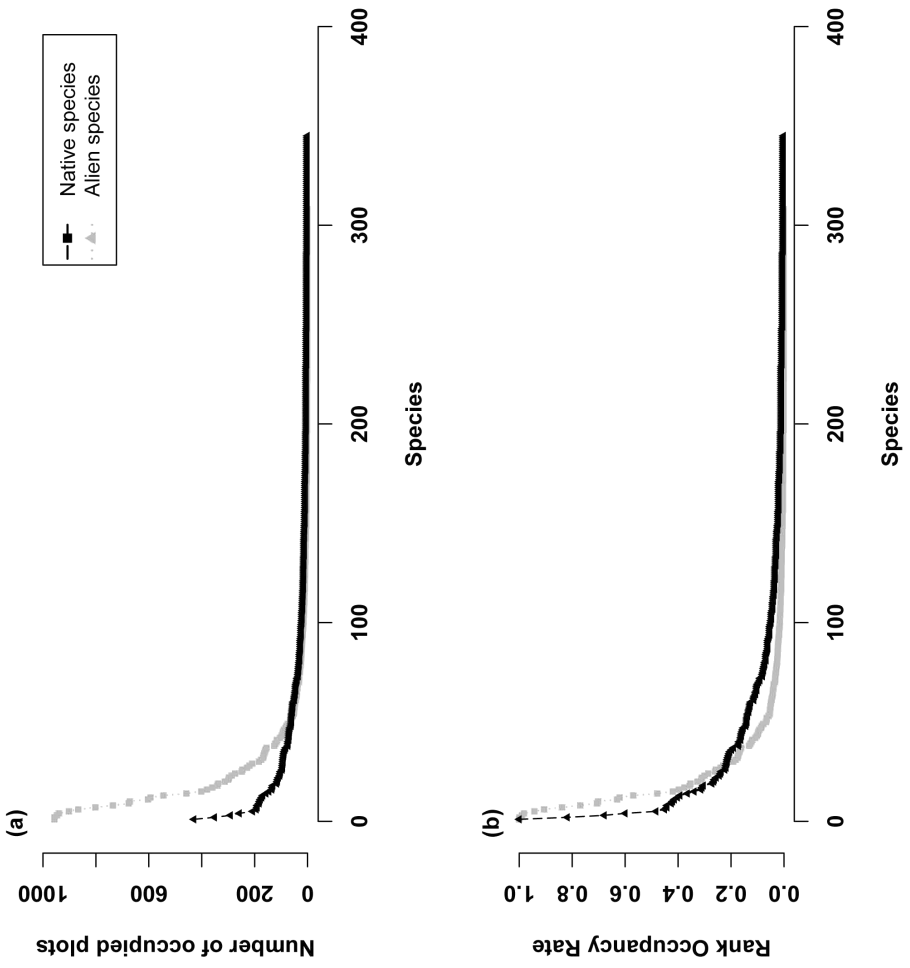

Figure 3.3. Occupancy Frequency Distribution - OFD (a) and Rank Occupancy Rate - ROR (b) of 368 native and 311 alien species on Banks Peninsula. The ROR is calculated by dividing the total number of the occupied plots for each species by the maximum of all occupied plots.

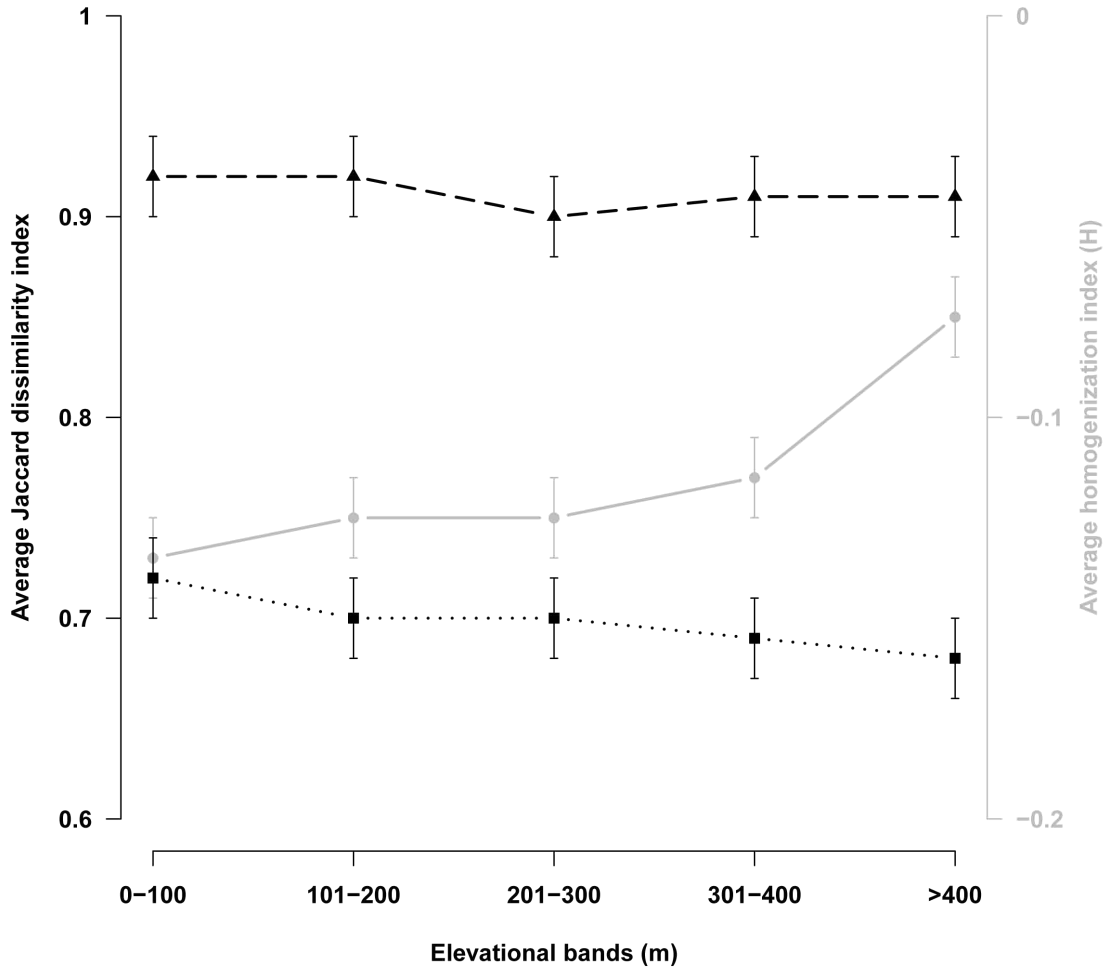

Figure 3.4. Changes in Jaccard dissimilarity index values (with 95% confidence intervals) of native (triangles) and alien (squares) dominated communities (black) within 5 elevational bands (0 - 100, 101 - 200, 201 - 300, 301 - 400, > 400 m a.s.l.). Changes in homogenization index values (*H*; with 95% confidence intervals) of all communities (grey) within elevational bands.

Within each elevational band this was confirmed but within each community type there were no significant differences in pairwise dissimilarity among communities (Figure 3.2). Along the entire elevational gradient, grass species such as *Rytidosperma clavatum* (430 occupied plots, average contributions to the dissimilarity = 94%), *Poa cita* (352, 88%) and herbs such as *Oxalis exilis* (292, 87%) were the most significant discriminating species that contribute to dissimilarity of the native dominated communities. This means that, for instance, in 94% of the plots where *Rytidosperma clavatum* is present, these plots tend to be mostly dissimilar to the other plots where *Rytidosperma clavatum* is absent. In the alien dominated communities, *Trifolium repens* (947 occupied plots, average contributions to similarity = 88%) and

Anthoxanthum odoratum (867, 95%) tended to be the most significant contributor species at low- to mid-elevations, while *Lolium perenne* (940, 92%) was the most significant at high elevations.

Pairwise comparison of plots in each of the elevational bands indicated a homogenization effect (negative H index from -0.15, at low-elevation, to -0.08 at mid- to high-elevation sites; Figure 3.4) by alien species on the Banks Peninsula plant composition. This was also confirmed by a positive relationship between alien species richness and the homogenization index found across the entire elevational gradient ($rho = 0.74$, $P < 0.05$). Homogenization effect was also evident in each of the community types (Figure 3.2). Where the community is dominated by at least 34% of alien species the homogenization effect was marked (negative H index from -0.12 to -0.27). Only in native second-growth forest and shrubland community (Type 8) there was a slightly no homogenization effect (positive H index of 0.06).

Patterns emerged also in the nestedness analysis. In general, native species communities were found to be less nested than alien communities ($NODF_n = 14.89$, $Z_n = 21.23$, $NODF_a = 43.45$, $Z_a = 25.7$, $P < 0.001$, respectively). This was also confirmed in each of the eight community types (Figure 3.2). However, if we randomize the presence of the species at every site but within their elevational range (see Methods), the nestedness of both native and alien species communities was found to be significantly higher in relation to increasing elevation, although native species communities were still less nested than alien communities ($NODF_n = 47.78$, $Z_n = 78.47$, $NODF_a = 52.54$, $Z_a = 42.35$, $P < 0.001$, respectively). This was also confirmed in analyses within each elevational bands with fewer nested native ($NODF_n = 5.41$) than alien ($NODF_a = 12.42$) dominated communities resulting at elevations > 400 m a.s.l.

3.5 Discussion

Previous studies of the native and alien plant species composition patterns in a disturbed landscape have shown that the native and alien species communities differ in their spatial and ecological distributions together with the environmental factors with which they are correlated (Wilson, 1989; Wilson *et al.*, 1989; Oneal and Rotenberry, 2008; Brown and Boutin, 2009; Otýpková *et al.*, 2011). In the Banks Peninsula montane outcrops (i.e. elevations > 500 m a.s.l.), Wiser and Buxton (2009) have already shown that the native and alien plant species community composition

is spatially segregated with more alien species occurring on the north-facing slopes than native species that occur more on the south-facing slopes. This geographic distinction of native and alien plant communities may be primarily due to elevational gradients that reflect climate differences, distinct orogeny on the Peninsula (Wilson, 2008, 2009) and the levels of human-related disturbances which lead to an invasion gradient. In my study across the whole Peninsula, I confirm that the variation in the native and alien plant species composition patterns is strongly related to the heterogeneous topography. Elevation itself is associated with the direct gradients of precipitation (which increases with elevation) and temperature (i.e. Growing Degree Days which decreases with elevation) with species arraying from warmer and drier plots containing typically more a mixture of alien grass and herbaceous species to cooler and wetter plots typically containing more native trees and shrubs. The relative importance of factors such as GDD, DEM, annual precipitation, distance to buildings and slope, principally characterize the community types (Figure 3.1, Figure 3.2, Appendix H). Types 1-2-3-4 (mainly alien species dominated communities) tend to occur on warmer and less steep plots with high solar radiation and closer to buildings, whereas types 6-7-8 (mainly native species dominated communities) are more likely to occur at cooler and steeper plots with low solar radiation and further away from buildings. Hence, at a large extent, Banks Peninsula plant communities are dominated by native and alien species which tend to be spatially separated and occupy different parts of the landscape (Figure J.1). The importance of elevation can be considered one of the major drivers of compositional variation of the flora on the Peninsula.

This elevational gradient also, but not completely, encompasses the dominant gradient that is the legacy of land-use history and management. A proxy measure of these human-related disturbances can be seen in the proportion of plots dominated by alien species. This leads to a marked invasion gradient which is mirrored by a shift in vegetation composition where a higher proportion of alien species per plot (93%), especially grass species (e.g. *Lolium perenne*, *Dactylis glomerata*, *Anthoxanthum odoratum*) is found (Figure 3.2). However, in less modified or regenerating areas a lower proportion of alien species per plot (i.e. 3%) is found, with the remaining plots occupied by a high proportion of native trees and shrubs (e.g. *Fuchsia excorticata*, *Kunzea ericoides*).

Elevational gradient is related to climate differences where native dominated communities are likely to be found in less modified or regenerating areas of native forest and shrubland occurring in less accessible and less productive cooler and

higher elevation south facing sites. Most of the forests prevail on south-facing slopes that are characterized by less productive sites. This is attributable not so much to land-managers wanting to convert the north-facing sites to pasture, but to the higher frequency of burning on the north-facing slopes than on the south-facing slopes (Williams, 1983; Wilson, 1998; Wiser and Buxton, 2008). This is the primary reason for forest removal on Banks Peninsula (Susan Wiser personal communication). Mid-elevation warmer sites tend instead to support more modified native dominated grassland species. In these less-modified areas, however, alien species may be less adapted to biotic conditions (e.g. competition for light and nutrients) and to less human disturbance (i.e. forest clearance and grazing) but not to the biotic resistance linked to the number of species present in the plots (see Chapter 4). Patterns of overall occurrence of species reveal that the native species pool has few species that are widely spread; these tend to be associated with tussock grasslands (e.g. *Rytidosperma clavatum* and *Poa cita*). However, a better adaptation to climate and soil pH on the Peninsula and the shift from grassland to remnant or regenerating native forest and shrubland lead to the remaining native species (e.g. *Melicytus ramiflorus* and *Coprosma rotundifolia*) occupying a relatively high number of plots, especially in those within native dominated communities (types 6-7-8).

Conversely, alien dominated communities are likely to be found in plots at warmer, lower elevation on northerly aspects where the magnitude of human-related disturbance may influence the species composition favouring highly productive fast growing alien species (for example *Lolium perenne* and *Trifolium* spp. swards; see Chapter 4). Patterns of overall occurrence of species confirm that the alien species distribution is strongly associated with human-related disturbances. This is highlighted by the fact that only few alien species (particularly highly-modified pasture; e.g. *Lolium perenne*, *Dactylis glomerata*) are present and dominant in 85% of the sites which are in grassland and where the land management levels (e.g. oversowing with pasture species and/or fertiliser addition to support extensive livestock grazing) are high. Alien species tend to occupy a high number of plots but only those highly influenced by human-related disturbances (types 1-2-3-4) to which they are usually more adapted. This reflects the fact that the remaining alien species occupy relatively few plots with types 1-2-3-4 that register higher OFD values than types 6-7-8 (Figure 3.3). Thus, the dominant gradients in native and alien vegetation patterns are driven and segregated by the vegetation changes that respond to the interplay of the climatic gradient and contemporary and historical human-related

disturbances (i.e. land-use and management) that covary along the elevational gradient.

Human-related disturbance, together with abiotic and biotic adaptation of both native and alien species that covary along the elevational gradient, may also account for the elevational zonation of native and alien species (Haider *et al.*, 2010). Although, overall, native species tended to occur at higher elevations than alien species, there was little evidence for any elevational separation of the most abundant native and alien species (Appendix I). Indeed, almost all alien species present at high elevation sites also occurred at lower elevation sites (community type 1-3). These patterns may be explained by the extensive sowing of alien species contained in a pool of desirable and contaminant seeds (mainly of pasture species such as *Lolium perenne* and *Dactylis glomerata*) that were sown across the Peninsula where a strong ecological filtering of alien species creates an alien assemblage containing few but dominant alien species (Godfree *et al.*, 2004). What we see are the survivors of this large extent experiment. Another reason can be found in the fact that most alien plant species initially establish at low elevations where propagule pressure is higher (Nogués-Bravo *et al.*, 2008; Pauchard *et al.*, 2009; Alexander *et al.*, 2011) and these need to be climatically pre-adapted to the climatic conditions (Dietz and Edwards, 2006) and from there, they then spread upwards either according to the time it takes for propagules to disperse to higher elevations (Ross *et al.*, 2008) or via human-related factors such as roads (e.g. *Silene gallica*) or via sowing. This is why alien pasture species adapted to cooler climatic conditions (e.g. *Lolium perenne*; Anderson, 1954) can grow at higher elevations where they are also maintained by management such as grazing and fertilizer application. Nevertheless, those processes may be also responsible for the restricted elevation distribution of native species at higher elevations. Human-related factors, in fact, are strongly present at low to mid-elevation sites where native species have been removed by forest clearance and fire leading the remnant native species pool (e.g. community type 8) to persist only at higher elevations or in less modified remnants of native forest vegetation [e.g. *Melicytus ramiflorus*, *Pennantia corymbosa* and *Schefflera digitata* can occur at lower elevations; Wilson (2009)]. However, the remaining native flora may also be present at mid- to high-elevations of the Peninsula due to the fact that those species are more adapted to abiotic conditions such as a cooler temperate climate in equilibrium with the environment and with the very complicated lithological and geological history over millions of years (Wilson, 2008, 2009). My results are consistent with a recent body of evidence (Pauchard *et al.*, 2009; Haider *et al.*, 2010; Alexander *et al.*, 2011),

which has found that high elevation floras tend to have species that are present at low-elevations in the same region, even though the climate may change dramatically along the elevational gradient.

Human-related disturbance may lead to further invasion by alien species and consequently to homogenization of native community composition because of "invasional meltdown" (Simberloff and Von Holle, 1999). In grassland (particularly improved alien pasture species), few dominating alien species establish in this new environment where native species have been removed. This can enable the invasion of other alien species which then may interact to facilitate others, creating a cycle that eventually benefits alien species and lead to homogenization of native community (Simberloff and Von Holle, 1999). The replacement of native species by alien species (especially improved pasture) as a result of contemporary and historical land-use and -management, and the spread of generalist cosmopolitan alien species has significant effects on the levels of biotic homogenization and community dissimilarity within species communities and within and across different elevational bands (Figure 3.4). Although the native dominated communities consistently show greater dissimilarity than alien dominated ones, the native flora has been homogenized by the spread of alien species. Land clearance and fire, along with high propagule pressure of alien species, tend to alter the species composition (Haubensak *et al.*, 2009). Therefore, any interpretation of these results is likely to be related to the legacy of land-use history and management levels that not only affect the native and alien species distribution but also the community composition, although there is no direct data to test this assumption. Although the homogenization effects of alien species are stronger along and within all the elevational bands, the results indicate that the degree of homogenization is relatively stronger in more highly disturbed habitats that are subjected to more intense human pressure or in more accessible and productive sites (typically at low- to mid-elevations; Figure 3.2). It is not surprising that alien dominated communities (Types 2-3-4) have a strong homogenization effect, especially at sites that are intensively managed through grazing, ploughing and fertilizer application which favour just a few highly productive fast growing alien species. The prevailing homogenization effect of alien species on floristic composition suggests that the majority of aliens established at these sites are cosmopolitan species, well-adapted to disturbed habitats. They are able to colonize all habitats with a similar regime and intensity of disturbance independently of whether they are located at low- or high-elevation sites. In contrast with the most disturbed habitats, differentiation effects do not invariably prevail over homogenization effects in less

disturbed sites (typically at higher elevations), except in native second-growth forest and shrubland community (Type 8) where differentiation is slight. The understory of plots dominated by native woody vegetation may be less susceptible to invasion by alien grass or herbaceous species which are better adapted to a more open environment and which consequently may show lesser homogenization effect. These findings support the hypothesis that biotic homogenization is a more serious problem for highly managed than for less managed areas (McKinney, 2006; Lososová *et al.*, 2012).

Why are alien dominated communities more highly nested than native dominated communities if there is little evidence for any elevational separation of the most abundant native and alien species? The traditional interpretation would be that alien species with similar environmental tolerances tend to be more closely related to higher human disturbance (e.g. community types 1-2-3; Figure 3.2). This is also confirmed by differences in their rank occupancy plots where alien species of improved pastures (such as *Lolium perenne*, *Dactylis glomerata*) occupy high numbers of plots but only because 85% of the Banks Peninsula landscape is grassland where the oversowing of pasture species and/or fertiliser addition are high. Along the elevational gradient, human-related activities are stronger at low- to mid-elevations where high intensity levels of land management (e.g. through grazing, ploughing and fertilizer application) favour just a few highly productive fast growing alien species (for example *Lolium perenne* and *Trifolium* spp. swards) which tend to be more nested than native species at these elevations. At higher elevations ($>$ 400 m a.s.l.), less intensive management may allow pastures to be invaded by other alien and native species; the nestedness of alien species, however, is still higher than native ones. The reason could be found in the hypothesis of Alexander *et al.* (2011), although their study was conducted at higher elevations than Banks Peninsula. This study showed that propagule pressure at high elevations is relatively low. Alien species that reach the highest elevations must be either good dispersers or may be spread and maintained by human-related activities. However, because they are able to establish populations across the full elevational gradient, the alien species pool may contain species with broader climatic tolerances. The nested patterns, therefore, may arise from a combination of decreasing propagule pressure related to human activities and a corresponding increase in the proportion of climatically generalist species with increasing elevation.

3.6 Conclusion

My results from a heterogeneous landscape provide strong evidence that the dominant gradients in vegetation and their associated underlying environmental factors (i.e. climate-topography and human land-use) vary along elevational gradients. The hypothesis that native and alien species patterns are spatially and ecologically segregated (i.e. occupancy and elevational range) is also confirmed. My study highlights that variation in abiotic conditions might explain a greater dissimilarity and nestedness within native dominated communities than in alien communities, even in the presence of lesser levels of disturbance. The levels of human-related disturbance primarily influence both native and alien species community composition and structure, offering, for example, the best conditions for the spread of alien species and consequently an increased homogenization effect of the native community. The role played by contemporary and historical human land-use and -management is critical and, even along a marked environmental gradient, it remains the main determinant of native and alien vegetation composition and structure. My results also demonstrated that where the recipient site is more disturbed biotic homogenization is stronger. This indicates that biotic homogenization is a more serious problem for highly managed than for less managed areas.

Chapter 4

Environmental gradients shift the direction of the relationship between native and alien plant species richness[1]

[1]Tomasetto, F., Duncan, R. P. & Hulme, P. E. (2013) Environmental gradients shift the direction of the relationship between native and alien plant species richness. *Diversity and Distributions*, 19:49-59. See Appendix K

"Which altitudes one should concentrate in controlling alien invasive species might be adjusted according to the different altitudinal distribution patterns." (Josè Ramón Arévalo)

4.1 Abstract

To assess how environmental, biotic and anthropogenic factors shape native-alien plant species richness relationships across a heterogeneous landscape we integrated a comprehensive floristic survey of over 1200 systematically located 6 × 6 m plots, with corresponding climate, environmental and anthropogenic data. General linear models examined variation in native and alien plant species richness across the entire landscape; variation between native and alien dominated plots; and variation within separate elevational bands. Across all plots there was a significant negative correlation between native and alien species richness but this relationship differed within subsets of the data: the correlation was positive in alien dominated plots but negative in native dominated plots. Within separate elevational bands, native and alien species richness were positively correlated at lower elevations, but negatively correlated at higher elevations. Alien species richness tended to be high across the elevational gradient but peaked in warmer, mid- to low-elevation sites while native species richness increased linearly with elevation. The negative relationship between native and alien species richness in native dominated communities reflected a land-use gradient with low native and high alien richness in more heavily modified native dominated vegetation. In contrast, native and alien richness was positively correlated in very heavily modified alien dominated plots, most likely due to co-variation along a gradient of management intensity. Both positive and negative native-alien richness relationships can occur across the same landscape, depending on the plant community and the underlying human and environmental gradients examined. Human habitat modification, which is often confounded with environmental variation, can result in high alien and low native species richness in areas still dominated by native species. In the most heavily human modified areas, dominated by alien species, both native and alien species may be responding to similar underlying gradients.

Keywords: Biological invasions, biotic interactions, climate, exotic species, land-use change, scale-dependence, weeds.

4.2 Introduction

Understanding the factors that underpin the relationship between native and alien plant species richness is of central importance in invasion biology because it provides a means to predict the vulnerability of ecological communities to invasion (Levine and D'Antonio, 1999; Lonsdale, 1999; Richardson and Pyšek, 2006) and the likelihood of impacts on biodiversity, e.g. biotic homogenization (Lambdon *et al.*, 2008; Winter *et al.*, 2009). There is an emerging consensus that the relationship between native and alien plant richness is scale-dependent, often being negative when assessed across small spatial grains and extents (i.e. scale of observation; Pyšek and Hulme, 2005) but positive as the scales of observation increase (Fridley *et al.*, 2004, 2007; Hulme, 2008). The explanation for this changing relationship, termed the "invasion paradox" (Fridley *et al.*, 2007), is framed in the context of a resident native community being invaded by alien species. For small spatial grains (e.g. plot size < 100 m^2) and small extents/scales (e.g. < 10 km^2), where the environment can be regarded as relatively homogenous and biotic interactions are likely to influence species co-occurrence, sites with more resident native species are better able to resist invasion by aliens through competitive exclusion, leading to a negative relationship between species richness (Levine and D'Antonio, 1999; Herben *et al.*, 2004). For larger spatial grains (e.g. plot size ≥ 100 m^2) and larger extents/scales (e.g. ≥ 10 km^2), encompassing greater spatial heterogeneity, variation in native species richness among plots primarily reflects the variation in underlying environmental conditions, including changes in resource availability, levels of disturbance or proximity to propagule sources (Stohlgren *et al.*, 2006; Fridley *et al.*, 2007; Hulme, 2008). Alien species should respond to these large-scale gradients in a similar manner to native species such that sites where conditions favour high (or low) native richness should likewise favour high (or low) alien richness, leading to a positive relationship between the two.

The evidence to date supports the expectation that native-alien richness relationships are positive at large plot sizes, which is usually interpreted as the result of both native and alien plant species responding to similar gradients in resource availability and habitat heterogeneity at a large extent (Stohlgren *et al.*, 2006). However studies that use small plots, while more suited to identifying patterns associated with biotic interactions between native and alien plant species, typically show more variable outcomes with both positive and negative relationships in common (Stohlgren *et al.*, 1999, 2006). This variability has been interpreted as a statistical problem associated with very small plots (1-10 m^2) that fail to adequately sample the plant community

resulting in high variance in native and alien plant richness due to high spatial turnover in species composition (Stohlgren *et al.*, 1999).

Nevertheless variability in the native-alien richness relationship might also arise for ecological reasons. A wealth of studies have highlighted that native and alien species can differ in their distribution, particularly in relation to anthropogenic impacts that can alter the representation of species through changes in the regional species pool via increased propagule pressure of aliens (McKinney, 2002; Arévalo *et al.*, 2005; Lockwood *et al.*, 2005; Aikio *et al.*, 2012), alterations of the disturbance regime through fire and grazing (Hobbs and Huenneke, 1992; D'Antonio, 2000; Keeley *et al.*, 2003), changes in soil nutrient status as a consequence of atmospheric or agricultural fertilization (Dukes and Mooney, 1999), other forms of land-management (e.g. highly managed or semi-natural pastures; Boughton *et al.*, 2011) or land-use history (e.g. ongoing reforestation; Parker *et al.*, 2010). Considerable effort has been invested in disentangling the role of environmental factors from anthropogenic factors in determining the richness of native and alien plants (Gilbert and Lechowicz, 2005; Carboni *et al.*, 2010; Bartomeus *et al.*, 2012), given that human pressure is generally correlated with better climate (Hanspach *et al.*, 2008; Marini *et al.*, 2009, 2012). While native and alien species richness can be positively associated along some anthropogenic gradients (e.g. human population density; Marini *et al.*, 2009), they can be negatively, or not associated, along others (e.g. land-management intensity; Boughton *et al.*, 2011). Consequently, positive and/or negative relationships between native and alien plant richness may be found within the same landscape depending on the character, magnitude and variation in the dominant environmental or anthropogenic gradients. In this study, we explore the relationship between native and alien plant species richness in over 1200 vegetation plots (36 m^2) systematically distributed across a heterogeneous landscape (*c.* 1000 km^2) on Banks Peninsula, New Zealand. The Banks Peninsula has a variable topography (0 to 920 m a.s.l.) associated with strong gradients in climate, land-use history and management, and distribution of human population. We used these data to address the following questions:

1. What is the overall relationship between native and alien plant species richness and how strongly is it shaped by variation in anthropogenic and environmental gradients?

2. Do similar native and alien relationships hold in plant communities that have either experienced relatively high or low human impact and are respectively dominated by either alien or native species?

3. What is the relative contribution of environmental and anthropogenic gradients to the relationship between native and alien plant species richness?

4.3 Materials & Methods

4.3.1 Study area

The Banks Peninsula study area is described in Chapter 2.

4.3.2 Floristic data

The comprehensive floristic survey conducted between 1983 and 1988 over the entire Banks Peninsula has already been described in Chapter 2. For the analyses here, we calculated the total number of native and alien species per plot, which we used as our response variables.

4.3.3 Explanatory variables

The values of 11 climate, environmental and human-related variables derived have already been described in Chapter 2.

4.3.4 Statistical analysis

All spatial data were stored and extracted using ArcGIS 9.3 (ESRI, 2009), and all statistical analyses were performed in R (2.13.0; R Development Core Team, 2012). We first quantified the relationship between native and alien richness across all plots using Spearman's rank correlation, because this measure is less sensitive and more robust than Pearson's correlation to outliers. Once we had verified that any outliers were not sampling errors, we then examined the relationship between native and alien richness separately for plots where the dominant plant species was either an alien or a native. We also assessed the correlations between native and alien species richness and the proportions of trees, shrubs, herbs and grasses because variation in the representation of these life-forms reflect a gradient in intensity of past land-use.

We then fitted a multiple regression model to identify factors that could explain the variation in native and alien species richness. To account for spatial autocorrelation, we fitted the regression models with a spatial autocorrelation structure using

generalised least-squares (GLS; Legendre, 1993; Dormann, 2007). We assessed the potential influence of spatial autocorrelation on parameter estimates by modelling different spatial correlation structures (Pinheiro and Bates, 2009) and using the Akaike Information Criterion (AIC; Akaike, 1974; Burnham and Anderson, 2002; Johnson and Omland, 2004) to identify the best model (Pinheiro *et al.*, 2011). We assessed the degree to which our models accounted for unexplained spatial variation by plotting a semivariogram of the normalized residuals.

We also examined whether explanatory variables showed a non-linear relationship to the response by testing for the importance of quadratic terms. Only soil pH showed a strong non-linear relationship with species richness, so we included this variable along with its quadratic term in the multiple regression model.

Given the large elevation range on Banks Peninsula and the covariance of anthropogenic impacts with elevation, we also examined how the native−alien species richness relationship varied across this gradient by examining the correlation between native and alien species richness separately for plots in five elevational bands ($0-100$, $101-200$, $201-300$, $301-400$ and >400 m a.s.l.) chosen to ensure that each band had an approximately equal number of plots. Stratifying plots by elevational bands ensures key climate variables (such as temperature and precipitation) remain within a narrow range and allows us to examine the relationship between native and alien richness having controlled for this variation (Hanspach *et al.*, 2008; Marini *et al.*, 2012, 2009).

4.4 Results

4.4.1 Relationships between native and alien species richness

Although slightly more native (368) than alien (311) vascular plant species were recorded in the 1227 plots on Banks Peninsula, on average over twice as many alien (16.4 ± 0.19) as native species (7.9 ± 0.23) were found per plot (Wilcoxon rank-sum test: $W = 120$, $P < 0.001$). Across all plots, native and alien plant species richness were significantly negatively correlated (Spearman's rank correlation, *rho* = -0.126, d.f. $= 1227$, $P < 0.001$; Figure 4.1a). However, fitting a cubic smoothing spline to the data suggested that the relationship was non-linear. For plots with fewer than about 10 native species, the relationship between native and alien richness appeared positive, while for plots with more than 10 native species the relationship was strongly negative. Over 60% ($n = 739$) of plots were classified as alien dominated,

with the majority being grassland plots dominated by introduced pasture species such as *Lolium perenne* (dominant in 189 plots), *Cynosurus cristatus* (89 plots) or *Dactylis glomerata* (83 plots). Alien dominated plots typically had low native species richness and comprised the majority of plots with fewer than 10 native species. The 488 plots dominated by a native species included modified tussock grassland dominated by *Poa cita* (94 plots) and *Rytidosperma clavatum* (52 plots), along with native forest and shrubland communities dominated, for example, by *Kunzea ericoides* (53 plots). Native dominated plots included the majority of plots with more than 10 native species. The separation of plots into those dominated by alien or native species largely accounted for the non-linear relationship between native and alien species richness seen across all plots (Figure 4.1a). For alien dominated plots, with low native but high alien species richness per plot (3.9 $\pm$ 0.15 and 17.5 $\pm$ 0.19, respectively), there was a significant positive relationship between native and alien richness ($rho = 0.26$, $P < 0.001$; Figure 4.1b). In contrast, the species richness relationship was stronger and significantly negative in native dominated plots ($rho =$ -0.34, $P < 0.001$; Figure 4.1c) with similar mean values of alien and native richness per plot (14.7 $\pm$ 0.36 and 14.1 $\pm$ 0.4, respectively).

Across all plots, the dominant species life-forms shift along the gradient of increasing native species richness. Plots with low native species richness have a higher proportion of alien grass and herbaceous species ($rho =$ -0.59, and $rho =$ -0.27, $P < 0.001$ respectively) while plots with high native species richness contain a higher proportion of native trees and shrubs ($rho = 0.59$, and $rho = 0.7$, $P < 0.001$ respectively, Table 4.1). These patterns remain when native and alien dominated plots are examined separately. Native dominated plots with low native species richness have a higher proportion of grass and herbaceous species ($rho =$ -0.69, and $rho =$ -0.39, $P < 0.001$ respectively), while those with high native species richness contain a higher proportion of tree and shrub species ($rho = 0.62$, and $rho = 0.69$, $P < 0.001$ respectively). For alien dominated plots, the same gradient is apparent where plots with high native species richness have a higher proportion of native tree and shrub species ($rho = 0.29$, and $rho = 0.51$, $P < 0.001$ respectively), while plots with high alien species richness have more grass and herbaceous species ($rho = 0.32$, and $rho = 0.37$, $P < 0.001$ respectively).

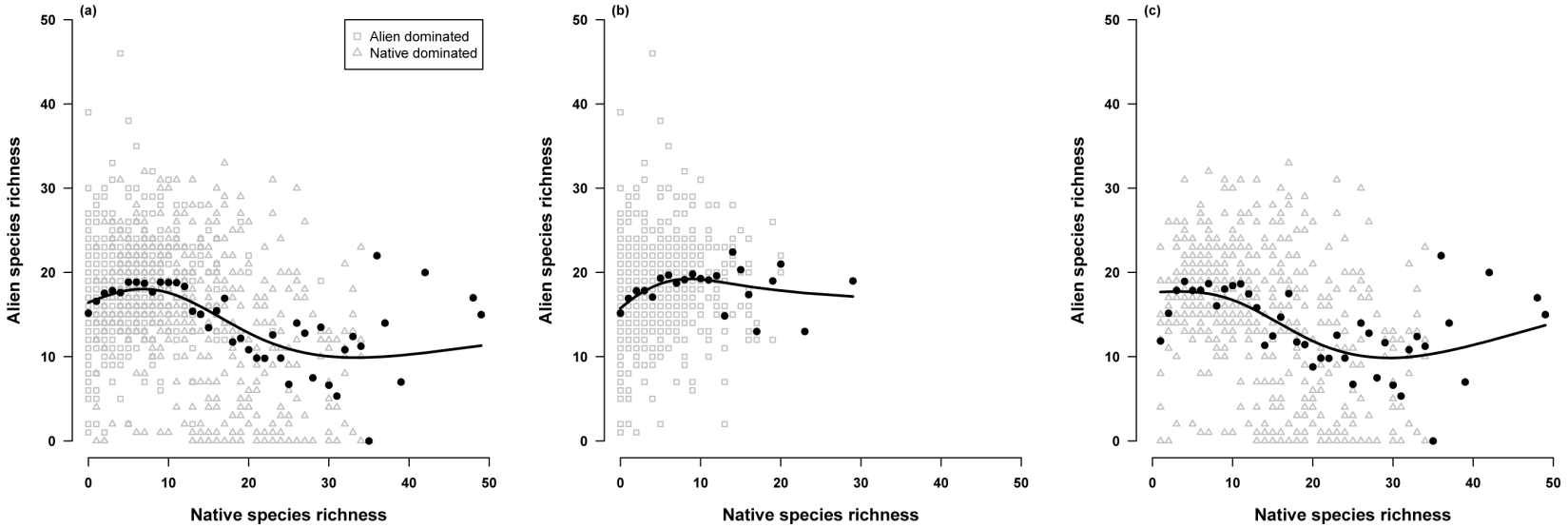

Figure 4.1. Relationship between native and alien plant species richness across the Banks Peninsula, New Zealand in: a) all 1227 plots (*rho* = -0.126, $P < 0.001$); b) Alien dominated plots (739 plots, *rho* = 0.26, $P < 0.001$); c) Native dominated plots (488 plots, *rho* = -0.34, $P < 0.001$). Grey points are individual plots; black points show the mean value of alien species richness for each value of native species richness. Solid lines show a cubic smoothing spline fitted to the full dataset.

4.4.2 Determinants of native and alien richness

Low but significant spatial autocorrelation was consistently found in the residuals of our GLS and thus we report results based on these spatial models. Plots with high native richness (containing a higher proportion of tree and shrub species) were more likely to occur at cooler sites (typically at higher elevation) with low solar radiation (steeper, south facing slopes), intermediate in soil pH, in areas with lower alien richness that were further away from unpaved roads (Table 4.1). In contrast, plots with higher alien species richness (dominated by grass and herbaceous species) occurred on warmer sites (typically at lower elevation) with high solar radiation (drier north facing slopes) that had low native species richness and intermediate soil pH (Table 4.1). Hence, at a large extent, plots with high native and alien species richness were spatially separated and tended to occupy different parts of the landscape. However, these edaphic factors only accounted for 21% and 9% of the variation in native and alien species richness respectively. Alien richness in the native richness model and vice versa explained a small, but significant amount of additional variation (increasing the variation accounted for to 23% and 11%, respectively; Table 4.1), indicating that unmeasured factors linked to biotic suitability further shaped species richness patterns.

These relationships were also evident within alien and native dominated plots (Table 4.1). Within each of these groups alien richness tended to be higher on warmer (lower elevation), drier north facing slopes while native richness tended to be higher on cooler (higher elevation) sites on south facing slopes, with both alien and native richness higher at intermediate soil pH and distant from streams. Alien richness was low and native richness was high, when there was a greater number of tree species per plot. The major difference was that, having controlled for other factors in the model, native and alien richness were positively associated in alien dominated plots (increasing the total variation accounted for from 14% to 21% respectively), but negatively associated in native dominated plots (19% to 25% of total variation accounted for). In addition, alien richness increased and native richness declined significantly with proximity to buildings in alien dominated plots, and with distance to streams in native dominated plots.

Alien species richness was generally higher than native species per plot across the elevation gradient (Table 4.2). However, native species richness increased with elevation for all plots and for plots dominated by either native or alien species, such that the only occasion mean native richness was greater than alien richness was at

the highest elevations (> 400 m) within native dominated plots. In contrast, alien species richness was less influenced by elevation and appears to have a unimodal relationship with a slight peak at at an elevational band between 101 and 200 m a.s.l. (Table 4.2). Across all plots, native and alien richness was significantly and positively associated up to 200 m a.s.l. but this relationship became increasingly negative at higher elevations, becoming significantly so above 400 m a.s.l. (Figure 4.2). Splitting the analysis into alien and native dominated plots separately revealed that this trend reflects the positive relationship between native and alien richness in alien dominated plots below 300 m a.s.l., and the negative relationship in native dominated plots above 300 m a.s.l. Within each elevational band and across the entire elevational gradient, there was a consistent positive relationship between native and alien species richness in alien dominated plots, and a consistent negative relationship in native dominated plots (Figure 4.2).

Table 4.1. Parameter estimates from multiple regression models [Generalized Least Squares (GLS) with spatial correlation structures] predicting: native and alien species richness within: 1) all plots (d.f. = 1227); 2) alien dominated plots (d.f. = 739), and 3) native dominated plots (d.f. = 488) with climate, environmental and human-related explanatory variables. In all cases, the explanatory and response variables were transformed ($\log_{10}[x+1]$) to ensure normality and to deal with zero values (see Chapter 2). Explanatory variables were then standardized to zero mean and standard deviation one so that parameter estimates were comparable. All explanatory variables (see Methods), were tested but only those variables that were statistically significant in at least one model are shown. Significant variables in a given model are shown in bold (*** $P < 0.0001$, ** $P < 0.001$, * $P < 0.05$). Also shown are the coefficients of determination (R^2), the total number of alien and native species (Total N), and the mean number of native and alien species per plot (Mean N) (± SE).

Variables	All plots		Alien dominated plots		Native dominated plots	
	Alien richness	Native richness	Alien richness	Native richness	Alien richness	Native richness
Total N	311	368	282	217	194	345
Mean N	16.4 ± 0.19	7.9 ± 0.23	17.5 ± 0.19	3.9 ± 0.15	14.7 ± 0.36	14.1 ± 0.4
Growing degree days	**3.39*****	**-2.99*****	2.01	**-2.61****	**3.11*****	**-5.26*****
Solar radiation	**0.87*****	**-1.44*****	0.04	**-0.86****	**1.28*****	**-2.12*****
Distance to buildings	-0.06	0.08	**-0.25****	**0.21***	0.11	-0.16
Distance to unpaved roads	0.09	**0.15****	-0.11	**0.17****	**0.15***	0.05
Distance to streams	**0.14****	-0.06	**0.21***	**0.21***	**0.17***	**-0.22****
Proportion tree/plot	**-0.33*****	**0.59*****	**-0.32*****	**0.29*****	**-0.61*****	**0.62*****
Soil pH	**1.96*****	**1.62*****	**2.05*****	**1.02***	1.25	**1.67***
Soil pH^2	**-1.28*****	**-1.05*****	**-1.34*****	**-0.65***	-0.83	**-1.08***
Alien richness	NA	**-0.58*****	NA	**1.41*****	NA	**-0.49*****
Native richness	**-0.18*****	NA	**0.75*****	NA	**-0.72*****	NA
R^2	0.11	0.23	0.14	0.21	0.19	0.25
Spatial correlation Structures	Spherical	Exponential	Exponential	Spherical	Exponential	Gaussian

Table 4.2. Total number of alien and native species and mean number of species per plot within: all plots, alien dominated and native dominated plots in each separate elevational band. Total number of plots in each elevational band are shown.

Elevational bands (m)	0 - 100		101 - 200		201 - 300		301 - 400		> 400	
	Alien	Native	Alien	Native	Alien	Native	Alien	Native	Alien	Native
All plots										
Tot. species	292	220	256	237	218	191	168	156	265	261
Mean species / plot	16.2	4.7	17.7	7.4	17.2	7.3	16.7	8.5	14.5	12.1
Tot. Plots	296		260		223		172		276	
Alien-dominated plots										
Tot. species	219	143	154	131	146	114	97	81	123	108
Mean species / plot	17	2.5	18.1	4.1	17.9	3.5	17.5	4.1	16.9	6.3
Tot. Plots	219		154		146		97		123	
Native-dominated plots										
Tot. species	68	73	100	105	67	76	69	75	135	151
Mean species / plot	13.1	11	16.9	12.3	15.8	14.4	15.7	14.2	12.6	16.7
Tot. Plots	77		106		77		75		153	

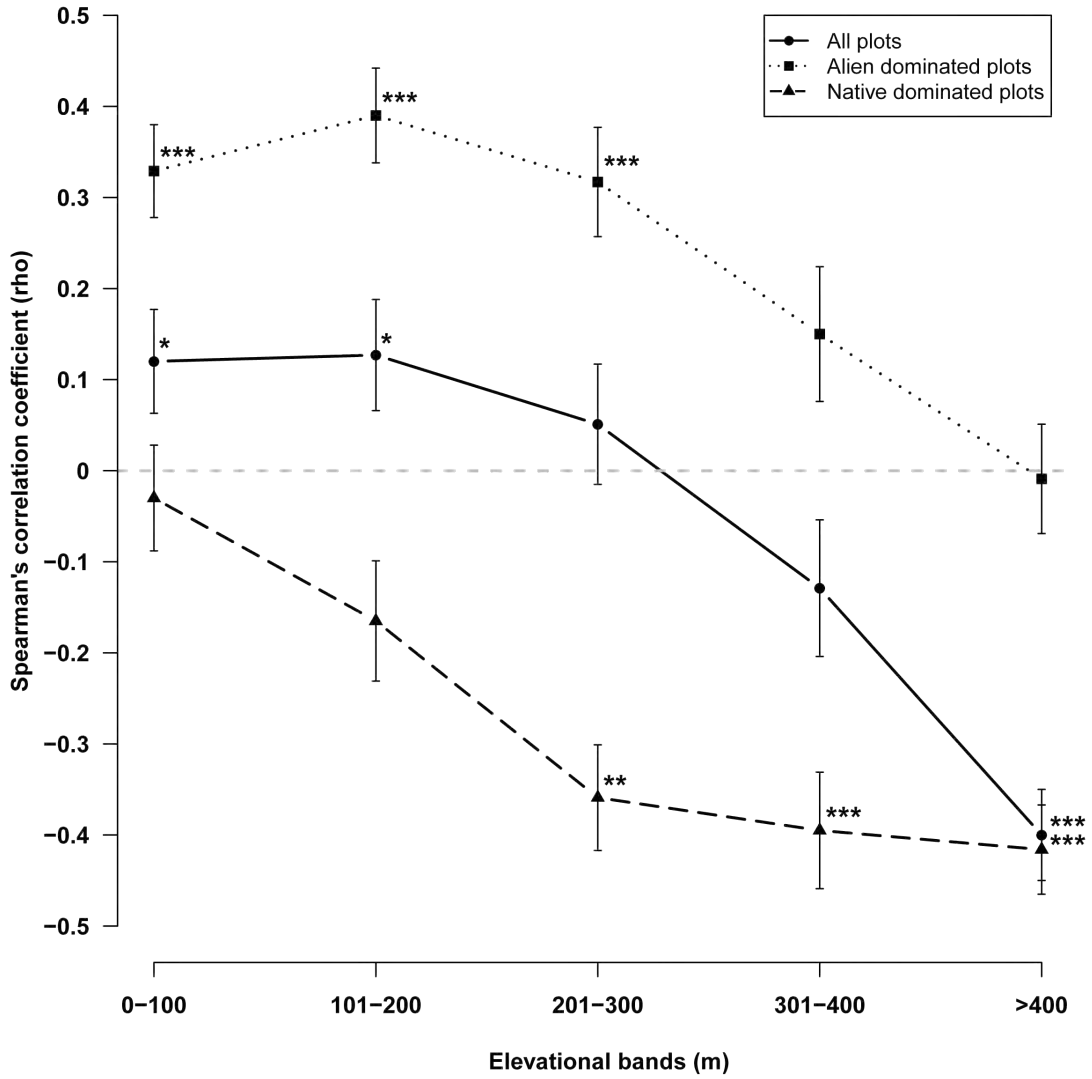

Figure 4.2. Change in Spearman's rank correlation coefficients (black dots with 95% confidence intervals) of native versus alien species richness within 5 elevational bands (0 - 100, 101 - 200, 201 - 300, 301 - 400, > 400 m a.s.l.). Solid line shows native-alien relationship within all plots ($n = 1227$). Dotted line shows native-alien relationship within alien dominated plots ($n = 739$). Broken line shows native-alien relationship within native dominated plots ($n = 488$). The horizontal dotted line shows value of $rho = 0$. The superscript refers to the statistical significance of correlations (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$).

4.5 Discussion

Previous interpretation of the sign and magnitude of the relationship between native and alien species richness has largely centered on the "invasion paradox" that addresses how the shape and strength of the native-alien richness relationship can change with spatial grain and extent (Levine and D'Antonio, 1999; Shea and Ches-

son, 2002; Fridley *et al.*, 2004; Herben *et al.*, 2004). We show, however, that at a constant grain and extent the relationship between native and alien richness differs between plant communities subject to relatively high or low human impact that are respectively dominated by either alien or native species. Such variation in the native-alien richness relationship at small plot sizes has previously been attributed to statistical problems associated with high turnover of species leading to high variation in species richness among plots and thus inconsistent relationships (Stohlgren *et al.*, 1999, 2006; Fridley *et al.*, 2007). Our data do show high among-plot variation in both native and alien richness (Figure 4.1) but we nevertheless find highly significant relationships with the sign of that relationship shifting from positive to negative in going from alien to native dominated plots. This shift could not be fully explained by changes in any of the environmental, climatic or human-related variables that we measured, although the explanatory variables did a consistently better job explaining native than alien richness. This might be expected if aliens were reasonably ubiquitous as a result of human impacts. Indeed, unlike other studies that typically find a marked decline in alien richness with increasing elevation (Alexander *et al.*, 2011; Marini *et al.*, 2011, 2012), we observed relatively little change (Table 4.2). Grasslands across the entire elevation range, for example, tended to contain a similar suite of common alien species (e.g. *Lolium perenne*, *Dactylis glomerata*, *Anthoxanthum odoratum*).

Within native dominated plots, the gradient of increasing native species richness coincided with a shift from plots at warmer, lower elevation on northerly aspects to plots at cooler, higher elevation sites on south facing aspects, with a correspondingly greater proportion of trees. This gradient most likely reflects a legacy of past land-use, with less modified or regenerating areas of native forest and shrubland occurring in less accessible and less productive higher elevation south facing sites, while mid-elevation warmer sites tend to support more modified native dominated grassland.

Why then is alien species richness negatively correlated with native species richness along this gradient? The traditional interpretation would be that high native richness drives the sign of the relationship and confers resistance to invasion by alien species (biotic resistance). However, while alien species richness declines along this gradient, plots with high native richness still have, on average, a high proportion of alien species (about one-half to one-third of species) suggesting these sites are readily invaded. This in turn may reflect the positive NARR ($rho = 0.29$, $P < 0.001$). Instead, it may not be high native richness per se that confers resistance to invasion, but the fact that higher native richness coincides with a shift from grassland to remnant

or regenerating native forest and shrubland. The understory of plots dominated by native woody vegetation may be less susceptible to invasion by alien grass or herbaceous species better adapted to more open environments, which comprise the bulk of the alien flora. This may reflect the negative NARR (*rho* = -0.24, $P < 0.001$). The lower number of alien species and the higher number of native species in these native dominated communities may thus reflect a shift in vegetation structure, from grassland to shrubland/forest, rather than being a function of biotic resistance linked to the number of species. Forested plots with high alien richness may also be in areas regenerating after agricultural abandonment, highlighting the potential for historical factors such as land-use change to influence current native-alien plant relationships (Parker *et al.*, 2010).

For alien dominated plots, we see a positive association between native and alien species richness, which is commonly attributed to both native and alien species responding in a similar manner to underlying environmental gradients associated with plant performance (Gilbert and Lechowicz, 2005; Richardson *et al.*, 2005). However, in our study, only one variable (soil pH) appeared to influence native and alien richness similarly (Table 4.1). None of the remaining environmental variables we measured could fully explain the covariance between native and alien species richness. Thus, is there any evidence that native and alien species richness covary along either anthropogenic or climate gradients?

Stratifying by elevation helps disentangle the potentially confounding effects of covariance among anthropogenic and environmental variables (Marini *et al.*, 2012). The relationship between native and alien species richness was consistently positive or negative for alien dominated and native dominated plots respectively even when the variation in climate was constrained within fixed elevational bands. This suggests that anthropogenic effects shape these relationships more strongly than climate. Nevertheless, the strength of the positive and negative relationships changed with elevation, suggesting that the magnitude of anthropogenic effects also vary with elevation.

In contrast to the findings of Boughton *et al.* (2011) who found management intensity resulted in negative relationships between native and alien species, we interpreted our positive relationship to be a function of the intensity of management. Sites with low native and alien species richness are dominated by alien pasture grasses that are intensively managed through grazing, ploughing and fertilizer application to favour just a few highly productive fast growing alien species (for example *Lolium perenne* and *Trifolium* spp. swards). Less intensive management may allow pastures

to be invaded by other alien and native species, leading to a positive relationship between the two, although aliens dominate in these more intensively managed systems. Thus, the positive relationship is driven by patterns in the persistence of native species along a gradient of management intensity which influences alien species richness to a much lesser extent.

With increasing elevation, climate variables might be expected to exert a greater influence on native and alien plant distributions and to affect these in a similar manner (Stohlgren *et al.*, 1999; Marini *et al.*, 2009; Pauchard *et al.*, 2009). However, across the large elevational gradient, while alien species richness showed a unimodal relationship that could be attributed to higher elevations becoming increasingly inclement, native richness progressively increased with elevation. While we might have expected a similar unimodal relationship for native species (Marini *et al.*, 2012), the linear relationship undoubtedly reflects the fact that much of the native diversity has been removed by forest clearance at low- to mid-elevations (Wilson, 2009). The outcome is that at low-elevation, where most plots are heavily modified and dominated by alien species, native and alien richness is positively correlated, while at higher elevations there is stronger spatial segregation, and hence a negative correlation, with less modified remnants of native forest vegetation tending to have more native and fewer alien species.

4.6 Conclusion

Much of the discussion to date regarding the drivers of native and alien species richness suffers from the fact that the grain and extent of studies are rarely independent and the grain size covaries with the spatial extent examined (Hulme, 2008). This prevents adequate assessment of the local-regional drivers on patterns of species richness. Our study is one of the few that examines patterns of species richness at a relatively fine grain (36 m^2) over a large spatial extent (*c.* 1000 km^2; c.f. Stohlgren *et al.*, 2006; Chen *et al.*, 2010). Our results do not provide strong evidence of biotic resistance associated with higher species richness limiting alien plant invasions, although this might only be expected to be found at even finer grain sizes (Levine and D'Antonio, 1999; Herben *et al.*, 2004). In contrast, our study confirms an increasing and recent body of evidence (Parker *et al.*, 2010; Boughton *et al.*, 2011) that indicates contemporary and historical anthropogenic impacts strongly shape both negative and positive relationships between native and alien species richness, especially where

such impacts covary with climate gradients. The impact of local management effects (e.g. land clearance, grazing) may be less discernible at larger grain sizes (> 1 km^2) where other large-scale environmental factors are likely to shape patterns in species richness.

Chapter 5

Native-alien plant species richness relationship: a global meta-analysis

"The patterns of native and alien species richness, one theory fits all or a plea for pluralism?" (J.D. Fridley)

5.1 Abstract

Ecologists have put considerable effort into documenting community invasibility using the native and alien species richness relationship (NARR). However, it is unclear whether this relationship can be subsumed under one theory or several, and which factors/moderators may underpin it. I present a quantitative meta-analysis from 112 articles reporting 193 case studies worldwide. Using multi-model inference within an information-theoretic approach combined with meta-regression analyses, I assessed the influence of 14 potential abiotic and biotic predictors to explain variation in the native and alien plant species richness relationship. An overall pattern of positive but non-significant native and alien species richness relationship at small spatial grains (plot sizes < 100 m^2) contrasts with significantly positive native and alien species richness relationship at large spatial grains (plot sizes > 100 m^2) and this is unlikely to be due to chance alone. Across all studies, a significant positive native-alien richness relationship was found with plot size consistently the best predictor. For studies sub-grouped by plot size, native-alien species richness relationship increases positively and significantly with increasing plot size. With regards to different habitat types, ecosystems and biogeographic regions there were no significant differences in the mean positive native-alien richness relationship. It is essential for purposes of conservation of native plant communities to focus our attention and efforts in habitats heavily invaded (e.g. forests and riparian areas). Future investigations of species richness on islands will further develop a quantitative approach to better understand native-alien richness relationship worldwide and help to clarify the "invasion paradox".

Keywords: Biological invasions, effect size, exotic species, habitat heterogeneity, meta-regression, scale, weeds

5.2 Introduction

Understanding the factors that underpin the relationship between native and alien plant species richness may provide key insights into the invasion process. In particular, the relationship between native and alien plant species richness (NARR) can be an ecological indicator for assessing community invasibility (Levine *et al.*, 2002), it provides a means to predict the vulnerability of ecological communities to invasion (Levine and D'Antonio, 1999; Lonsdale, 1999; Richardson and Pyšek, 2006) and the likelihood of impacts on native species richness (e.g. biotic homogenization; Lambdon *et al.*, 2008; Winter *et al.*, 2009). While numerous studies have shown that the number of alien species establishing in a community is related significantly to the native species richness of that community [reviewed by Lonsdale (1999)], the strength and direction (whether positive or negative) of the relationship often varies markedly among studies and there is an on-going debate as to whether such variation in the relationship between native and alien species richness can be subsumed under one theory or several (Fridley *et al.*, 2007).

Studies that report a negative NARR are usually interpreted as supporting the biotic resistance hypothesis, whereby species-rich communities are more resistant to the establishment of alien plant species than species-poor communities (Elton, 1958; Lodge, 1993), resulting in less invaded ecosystems. This can be seen as the result of the interplay between ecosystem saturation (Schwartz *et al.*, 2000) and the "Niche Differentiation Hypothesis" (MacArthur and Levins, 1967) or limiting similarity that is often related to the prerequisite of niche differences (Pacala and Tilman, 1994; Chesson, 2000). Species assemble because they have different niches which are complementary and can coexist. In native species-rich ecosystems, the more niche space is filled by native species resulting in a saturated ecosystem, the less alien species can invade it, leading to a negative NARR (Fargione *et al.*, 2003). In case of unsaturated ecosystems, the Niche Differentiation Hypothesis may also lead to an independence of native and alien species richness (Gerhold *et al.*, 2011). For instance, alien species, which have contrasted set of traits compared to native species, can invade and fill empty niches because these are left "unused" by native species and leading to a positive NARR (Stohlgren *et al.*, 2008).

Other studies have instead shown the exact opposite, namely a positive NARR, which has been termed the biotic acceptance hypothesis [(Stohlgren *et al.*, 2006; Fridley *et al.*, 2007; Bartomeus *et al.*, 2012) and references therein] because it indicates that sites with high native species richness are the most readily invaded

by alien species. The biotic acceptance hypothesis lies behind in the Grime's theory (Grime, 1973), where all species respond similarly to both stress competition and disturbance regardless whether they are native or alien species.

These contradictory relationships, in the context of a resident native community being invaded by alien species, have been termed the "invasion paradox" (Fridley *et al.*, 2007). However, there is an emerging consensus that changes in the direction and strength of NARR can be explained by the shift from biotic to environmental drivers of plant community structure and that this is related to increases in the spatial grain and extent of studies (Fridley *et al.*, 2007), where the spatial grain is the size of the recording unit (i.e. plot size) and the extent is the size of the study area (*sensu* Hulme, 2008). The function defines of both spatial grain and the extent is the scale of observation (Pyšek and Hulme, 2005).

A fundamental aspect of NARR is, in fact, that it is scale-dependent. At small spatial grains and extents/scales (i.e. small plot size in a single plant community), NARR is often negative but becomes more positive as the grains and extents of observation increases (Fridley *et al.*, 2004, 2007; Hulme, 2008). At small spatial grains and extents, biotic and environmental drivers of community composition can be hypothesized to be relatively homogenous, and biotic interactions (e.g. competitive or facilitative interactions *sensu* Fridley *et al.*, 2007) may be the main factors in explaining native and alien species richness. At these scales, and relative to species poor communities, species rich native communities may use more of the available resources by occupying more of the available niche space, leading to competitive exclusion of alien species and a negative NARR. As the plot size and extent increase, and plots sample a wider range of environments, variation in environmental conditions (spatial heterogeneity) rather than biotic interactions may drive the distribution of both native and alien species, with sites environmentally suited to high native species richness also favouring high alien species richness. Hence, environmental variation may explain more of the variation in NARR, while biotic interactions become less important, as the spatial grains of sampling increases, leading to an increasingly positive NARR (Levine and D'Antonio, 1999; Byers and Noonburg, 2003; Davies *et al.*, 2005). In addition, some plots may be closer to disturbance and propagule sources, and have more resource availability than others, facilitating higher richness of both native and alien species at these large spatial grains and extent (the so-called "the rich get richer" paradigm; Fridley *et al.*, 2007). Both processes may operate in the same landscape, with negative NARRs found at small grains and extents within local communities, but a positive NARR emerging across communities due to different

environmental conditions when assessed at a large spatial grains and extents (Shea and Chesson, 2002; Bartomeus *et al.*, 2012). Furthermore, at large extent, higher probabilities of colonization and lower probabilities of extinction, which are dynamic and variable across time, foster higher total numbers of both native and alien species (MacArthur and Wilson, 1967). This would lead to an overall positive NARR at these large spatial grains and extents.

In addition to differences in spatial grain and extent found in studies, other important factors might also influence the strength and direction of NARR. Significant factors of NARR at different spatial scales might be found in the "Niche Differentiation Hypothesis" (MacArthur and Levins, 1967) and the "Habitat Filtering Hypothesis" (Keddy, 1992). The "Niche Differentiation Hypothesis" suggests that alien species differ from native species in specific traits that allow the alien species to fill different niches and as a result exhibit different community trait distribution patterns (Rejmánek and Richardson, 1996; Lambdon *et al.*, 2008). The "Habitat Filtering Hypothesis" suggests instead that alien species have pre-selected traits that allow them to be pre-adapted to the new environment, with some successful alien species sharing similar traits to native species. A global study of plant traits has observed functional differences between native and alien species both at the local and the global scale (Van Kleunen *et al.*, 2010). This may lead to different sign and magnitude of NARR according to the spatial scale of observation. At small spatial grains and extents, the Niche Differentiation may allow the coexistence of native and alien plant species (Levine *et al.*, 2004). However at these small spatial grains, biotic interactions such as competitive exclusion may be held and this might lead to a negative NARR. In contrast, at large spatial grains and extents or along marked altitudinal/environmental gradients, Habitat Filtering may limit both native and alien species occurrence with both species exhibiting similar traits (Marini *et al.*, 2012), and this may lead to a positive NARR at these large spatial grains and extent (Gross *et al.*, 2013).

As well as differing in spatial grain and extent among studies, NARR might be expected to change through time depending on the different invasion stages (i.e. transport, colonization, establishment and spread; *sensu* Theoharides and Dukes, 2007) where different factors determine invasion dynamics (Clark and Johnston, 2011; Clark *et al.*, 2013). For instance, Clark *et al.* (2013) demonstrated, via simulation models, that temporal change of NARR may occur in any spatially structured system where species compete for resources and are subject to disturbance. This study showed that a negative NARR occurs when the probability of alien species

colonizing an area is inversely related to the density of the native species. In fact, at early stage of invasions, alien species may be advantaged by disturbance while native species may be reduced leading to a negative NARR. In contrast and at a later stage, a positive NARR is the result of both native and alien species responding similarly to the same processes (e.g. disturbance, dispersal and recolonization).

Biotic factors such as the number of native and alien species richness per plot and total species richness may also shape NARR. Unless native and alien species contrast significantly (e.g. different life-forms), factors controlling native species richness should similarly control alien species richness (see Chapter 3, Chapter 4), with the number of native species that may be assumed to be an indicator of biotic but also abiotic conditions favourable to invasion leading to a positive NARR (Levine and D'Antonio, 1999). Therefore, NARR may be expected to reflect the mean number of species per plot as a result of the random processes present (Herben *et al.*, 2004). In an experimental study, Herben *et al.* (2004) showed that the sign and magnitude of NARR varied as function of mean number of native and alien species per plot where NARR might be expected as a result of random processes due to this dependence of NARR to species richness on an area. Where in many areas, more heterogeneity in abiotic conditions with a net increase in species (i.e. total species richness) is found, this may also lead to a positive NARR (Stohlgren *et al.*, 1999), although the mechanisms related to NARR for total species richness are not clear (Davies *et al.*, 2005). Positive NARR may also be explained by the ratio between alien and native species richness (namely ANR), that is the threat of biological invasions to native diversity or the level of invasion [*sensu* Hulme (2008); Lonsdale (1999); Chown *et al.* (2005); Marini *et al.* (2009) and references therein]. Chen *et al.* (2010) found that in a wetland community of USA, a high level of invasion leads to stronger positive NARR. They attributed this positive sign of NARR to the establishment and invasion by alien species (with a potential homogenization effect) of a rich-native community, but whether this can be applied to other plant communities worldwide is unknown.

Abiotic factors such as environmental heterogeneity (i.e. habitat diversity) may also shape NARR. It may be the case that the number of coexisting species in a region is dependent on the magnitude of the habitat diversity within that region (Fridley *et al.*, 2007). Low habitat heterogeneity, limited resources which are completely used, and more apparent effects of species competition lead to invasion resistance (i.e. negative NARR; Morgan, 1998; Stachowicz *et al.*, 2002; Fridley *et al.*, 2007). In contrast, high habitat heterogeneity with great species composition and environ-

mental conditions leads to biotic acceptance (*sensu* Stohlgren *et al.*, 2006) with a resulting positive NARR (Levine, 2000; Davies *et al.*, 2005).

Covarying factors such as different habitat types, ecosystems and biogeographic regions may also change the sign and magnitude of NARR. For instance, open grasslands as well as riparian/wetlands zones may be more susceptible to invasion than forests due to the availability of light, water and nutrients (Stohlgren *et al.*, 1998; Stohlgren, 2002; Maskell *et al.*, 2006; Pyšek *et al.*, 2010a; Fridley, 2011). Forests have in fact historically been considered largely resistant to invasion (Wiser and Allen, 2006). A slightly significant negative NARR in riparian zones (Stohlgren *et al.*, 1998) contrasts with a stronger positive NARR in wetland zones (Chen *et al.*, 2010). Another example of changes in NARR sign and magnitude within different habit types can be found in Stohlgren *et al.* (1999) where the authors found a negative relationship in the Central Grasslands but a positive trend in the Colorado Rockies (USA). Differences of NARR revealed in grassland and forests worldwide are unknown.

The NARR may also vary across one or many ecosystems. Darwin (1859) and Elton (1958) suggested that lack of intense interspecific competition on islands made these low-diversity habitats more susceptible to invasion compared with mainlands (Gimeno *et al.*, 2006; Pyšek and Richardson, 2006; Stohlgren *et al.*, 2008). Hulme (2004) highlighted how the higher vulnerability of islands relative to their mainland counterparts can be attributed to a series of factors such as proportionally lower number of native species, the existence of unsaturated communities and the higher susceptibility of insular species to the ecological impacts of invaders. However, Vilá *et al.* (2010) found that para-oceanic islands (i.e. historically connected to a continent) were less invaded than their mainland counterparts, probably due to differences in landscape heterogeneity and propagule pressure. We need to bear in mind these contradictory findings and the fact that the sign and magnitude of NARR in relation to the number of native and alien species in island flora is unknown. The biotic resistance and the biotic acceptance hypotheses may also play a role here in the local NARR and so emphasize the importance of studying the invasion process in those ecosystems if we aim to assess NARR worldwide.

Biogeographic regions such as North America and Europe are particularly well investigated in invasion ecology. In Europe, more introduced species than in North America can be encountered due to a higher degree of human affiliation with introduced species coevolving over time with the native plants and pathogens [(Di Castri, 1989; Fox, 1990; Jeschke and Strayer, 2006) and references therein]. The findings

that grasslands in North America are more invaded than the corresponding communities in Europe (Seastedt and Pyšek, 2011), contrasts with the "resistance hypothesis" which states that the less disturbed and richer North American biota offers more resistance against alien plants than the European biota (Elton, 1958; Brock *et al.*, 1997; Levine and D'Antonio, 1999). To my knowledge, hypotheses about NARR and any difference in the sign and magnitude between these regions have not been advanced. This leaves a significant gap if we are to fully understand the vulnerability of ecological communities to invasion at a global scale.

Human-related factors (i.e. disturbances) are also likely to be a key contributor to NARR variation (Herben *et al.*, 2004; Fridley *et al.*, 2007). NARR sign and magnitude may change according to land-use history (e.g. positive NARR can be found in young forests converted from agricultural areas; Parker *et al.*, 2010) and land management intensity (e.g. negative NARR in semi-natural wetlands but no significant NARR in highly managed wetlands; Boughton *et al.*, 2011). NARR sign and magnitude may also change within the same landscape depending on the character, magnitude and variation in the dominant environmental or anthropogenic gradients (e.g. positive NARR in alien-dominated but negative in native-dominated communities; see Chapter 4).

Earlier review articles on NARR (Herben *et al.*, 2004; Fridley *et al.*, 2007) have discussed only a few of these factors (e.g. plot size and extent, native and alien species richness, habitat heterogeneity) and gaps still remain in our understanding of NARR. Stohlgren *et al.* (2006) have attempted to examine the continuum of relationships between native and alien species at multiple spatial grains (i.e. plot size) and habitats, and they found NARR to be scale dependent. The findings of more positive and significant NARR with increased plot size and extent can be attributed to biotic acceptance or to a multitude of factors that covary with spatial and temporal scales such as climate, disturbances, resource availability, species pools and propagule pressure. However, this study was restricted to areas in the central US and cannot easily be extrapolated to a global scale. Furthermore, these studies were either observational (Stohlgren *et al.*, 2006) or conceptual/theoretical (Fridley *et al.*, 2007) or relied on simple "vote counting" approaches to measure the overall trends emerging from multiple studies (Herben *et al.*, 2004). In the latter case, the influence of a variable was assessed by weighing the number of studies that showed significant results for its effect against those that did not (Gurevitch and Hedges, 1999; Gates, 2002). No quantitative estimate of the effect of interest (i.e. effect size) is provided by vote counting and it lacks statistical power (Osenberg *et al.*, 1999;

Harrison, 2011). Consequently, leading meta-analysts deplore its use (Gurevitch and Hedges, 1999; Borenstein *et al.*, 2009).

Thirteen years after Levine & D'Antonio's review study on the linkage between biological diversity and invasion, it is clear then that gaps in our understanding of NARR still remain, whether, for instance, NARR is scale dependent worldwide or if it changes between habitats types, ecosystems and biogeographic regions. I used quantitative meta-analysis techniques to explore the heterogeneity (i.e. real differences between studies calculated as the presence of variation in true effect sizes; Higgins *et al.*, 2003) of NARR and to identify large-scale processes and patterns (*sensu* Stewart, 2010) across results from multiple studies worldwide and so to address some of those gaps. Previous review articles have used no more than 23 observational studies involving sample units of a fixed grain. I applied rigorous and quantitative techniques to assess the influence of selected factors (the so-called moderators in meta-analytic literature) to explain the variation in NARR in 112 articles obtained from the literature. The factors chosen include: number of plots/grid cells, plot size, extent, total species richness, mean native and mean alien species per plot/grid cell, ANR and habitats/land cover types. I also evaluated the relative importance of these factors in explaining variation in NARR having controlled for the effects of plot size. More specifically, I examined two key questions in this chapter:

1. What moderators explain the variability in NARR at a global scale?
2. What moderators are important in explaining variation in NARR when studies are stratified by plot size?

5.3 Materials & Methods

5.3.1 Literature search

My study draws on quantitative evidence from the literature on NARR from all over the globe. I searched for relevant articles on the ISI Web of Knowledge database (http://apps.isiknowledge.com) on 10th April 2012 with no restriction on publication year, using the following search term combinations: (native plant* OR endemic plant* OR indigenous plant*) AND (non-native plant* OR non-indigenous plant* OR alien plant* OR exotic plant* OR weed*) AND (species richness OR species diversity* OR species composition OR homogen* OR invasib* OR plant invasion*). I screened the reference lists from all retrieved articles for other relevant publications including previous reviews (e.g. Levine and D'Antonio, 1999; Herben *et al.*, 2004; Fridley *et al.*,

2007). I also used abstracting service tools (BIOSIS, JSTOR, ProQuest Dissertations Publishing, Science Direct, Scopus) and internet web searches (e.g. Google Scholar).

I examined over 12000 articles to assess their potential for meeting several selection criteria for inclusion in the analysis. The main selection criterion required studies to have quantified the native and alien plant species richness within multiple sample units of a fixed grain (i.e. plots or grid cells). Selected studies were also required to provide details of the relationship (correlation or regression coefficients) and/or the actual data (in tables or figures). Studies that measured native and alien species richness at a state or county-level, or at the level of entire islands, and/or those which primarily used source annotated checklists were excluded because samples were not assigned to units of a fixed area.

This resulted in an initial set of 221 articles from which the following criteria for data inclusion were adopted:

1. The study object had to be relevant, i.e. population only of terrestrial and vascular plants excluding bryophytes, algae or fungi. Studies were included irrespective of grain-size (i.e. plots or grid cells) and extent, ecosystem and habitat type. Because the scope of the present study was intended to be global, I made an informed decision to consider studies from all the continents and from islands only where unit of fixed grain was used, and to consider NARR across different locations with similar habitats and ecosystems. Studies excluded = 30

2. Only results from non-manipulated (i.e. non-experimental) plots were considered. It may be difficult to produce general theories of invasion for landscapes and regions by evaluating processes at very local scales (i.e. plant neighbourhood) where the number of plant species used in experiments is usually quite small relative to the number of species in the regional species pool (Stohlgren *et al.*, 2002) or the complexities-related to natural ecosystems are rarely included (Fridley, 2011). Moreover, the type, size and age of the selected species are often restricted in experiments (e.g. short-lived grasses and herbs), as are habitat heterogeneity, environmental gradients (e.g. one vegetation type and biome) and levels of spatial and temporal scale (e.g. neighbourhood-scale and short terms; Stohlgren *et al.*, 2002; Fridley *et al.*, 2007). Studies excluded = 30

3. The number of native and alien species were obtained from complete species lists or from at least a part of them, but restricted to the fact that alien status was

considered according to the definition of Pyšek *et al.* (2004). This pre-requisite allowed me to test NARR according to broader and reliable categories (i.e. native versus alien species) rather than be restricted to only a small percentage of these naturalized alien species which had become invasive. Studies excluded = 20

The response variable was the regression or correlation coefficient derived from the NARR. Where the NARR was recorded for the same plots but in multiple years, I used only the chronologically most recent dataset to avoid pseudoreplication. There was one instance where the same dataset was used in two publications (Pino *et al.*, 2005; Bartomeus *et al.*, 2012), the most recent publication was used. Studies excluded = 1.

5.3.2 Data extraction

A total of 112 articles representing 193 cases of invasion across all of the world regions (excluding Antarctica) met my criteria (Appendix L). This sample size is an order of magnitude greater than previous reviews of NARR (Herben *et al.*, 2004; Fridley *et al.*, 2007). Firstly, and where readily available, I extracted either the Pearson product-moment correlation coefficient (*r*) or Spearman's rank correlation coefficient (*rho*) and mean native and alien species richness. Where these were not readily available, I extracted variables such as native and alien plant species richness per plot and their statistical variation (usually SE) from graphs (e.g. scatter plots or histograms) using DATATHIEF III software (Thumers 2006; available at http://www.datathief.org). Where published studies provided graphs representing the number of native and alien species and their relationships using logarithmic or square-root transformed scales, I back-transformed the data prior to analysis. In a number of cases, the published studies did not provide correlation coefficient estimates for non-significant results. In these cases, the published data were either re-analysed or I transformed the published test statistics (e.g. F or χ^2 tests) into the effect size as Fisher's z (Del Re, 2012). I also extracted the mean number of species and the associated statistical variation, plot size, spatial sample size (i.e. number of plots/grid cells) and spatial extent from each of the studies. Where these data were not available in the publication I obtained data directly from the corresponding authors of the studies (48 contacted, 20 replied).

5.3.3 Moderators

From the pool of studies, I either extracted or calculated the following moderators (i.e. potential predictors in meta-analytical studies *sensu* Thompson and Higgins, 2002) to objectively assess the influence of these factors to explain the variation in NARR:

1. *Number of plots*. The number of plots/grid cells which have been used in each study

2. *Plot size*. Bearing in mind that NARR is scale-dependent, I classified each study by plot size, which is the size of the sample plots converted into km^2, and used this in the study. Having gathered consistent, multi-scale data across all world regions, I then quantified NARR and the potential variables affecting it separately for three sub-groups of sample plot sizes (0.1 - 10, 11 - 100, and > 100 m^2)

3. *Extent*. I calculated the size of the study area (km^2) over which the samples were collected or, alternatively, when the study was conducted in plots along a transect, I calculated the maximum distance between the two most distant transects (i.e. length of the study area) and the breadth of the transect (i.e. width of the study area) where these were parallel to each other. Where the study area was sampled by a unique transect, I used the maximum distance between the two most distant plots within the transect (i.e. its length) and the width of the plot. These were then converted into an area (km^2)

4. *Total species richness*. This moderator was calculated as the sum of alien + native plant species sampled in each study

5. *Mean native* and *alien species richness*. The overall mean native and alien species richness per plot was calculated and used as moderator

6. *Alien Native Ratio* (ANR). I calculated the ANR, as the ratio of the total of alien to native species richness

7. *Habitats/land-cover types*. I determined the habitats/land-cover types encountered in each study. Where no habitat was mentioned in the study, I determined, using GIS tools (ESRI, 2009), the number of habitats and which habitats were present using the global land-cover types classification data (Hansen *et al.*,

2000) as these are reliable surrogates for habitat (the occurrence of a species is strongly correlated with the occurrence of its habitat; Fleishman *et al.*, 2006). Although in some cases, this habitat classification may under-estimate the number of habitats when compared with those directly determined in the study, this allowed me to assess the habitat heterogeneity in large spatial grains and extents studies.

In addition to the effect size and the first set of moderators, where possible, each study was objectively classified with respect to levels of ecological complexity (e.g. different habitat types, ecosystems and biogeographic regions). The following moderators may play a role in explaining the variation of the effect size.

1. *Forest* versus *Grassland* versus *Riparian*. Where possible, I classified each study as grassland, forest or riparian habitat. Only studies that were exclusively conducted in one of these three habitats were considered, excluding studies conducted in multiple habitats. I then tested if NARR differed between these habitat types. I tested this after I merged studies of riparian and wetlands areas, as these habitats are often associated in their vulnerability to invasion (Vitousek *et al.*, 1997; Richardson *et al.*, 2007)

2. *Islands* versus *Mainland*. I tested the magnitude of NARR from island ecosystems and compared these with those from mainlands. I assumed that mainlands were a large continuous extent of land that includes the greater part of a country or territory, as opposed to offshore islands (OED definition)

3. *North America* versus *Europe*. North America and Europe are particularly well investigated regions from a perspective of plant invasions (Pyšek *et al.*, 2008). I tested if NARR may be more strongly positive in studies from Europe than North America (defined as Canada and the United States excluding Hawaii). To conduct this comparison, I compared studies conducted in Europe and North America.

5.3.4 Data analysis

I performed meta-analyses using the packages *meta* (Schwarzer, 2010) and *metafor* (Viechtbauer, 2010) in R 2.15 (R Development Core Team, 2012). Data were analysed using random-effects models which are preferable in ecological data synthesis

because their assumptions are more likely to be satisfied (Gurevitch and Hedges, 2001; Harrison, 2011). Random effects meta-regression analyses were conducted to assess the relationships between moderators and the true effect sizes between all studies. I assessed the relationships between moderators and the true effect sizes between studies having grouped plots into three classes on the basis of plot sizes (i.e. sub-groups; *sensu* Borenstein *et al.*, 2009). There were no statistically significant relationships between moderators classified with respect to levels of ecological complexity and effect sizes. Consequently, I excluded all of these non-significant moderators from the results.

I used the unweighted (i.e. random-effects) regression because it is often more reliable than weighted (i.e. fixed effect) regression (Fletcher and Dixon, 2012). I also assessed heterogeneity by visual inspection of forest plots (i.e. graphical representations of a meta-analysis). Although heterogeneity is inevitable in a meta-analysis, this can be formally tested using Q and I^2 (Thompson and Sharp, 1999), to determine whether there is an "acceptable" degree of heterogeneity (Higgins, 2008). Publication bias was assessed both graphically, using funnel plot asymmetry, and statistically with Egger's regression test (Egger *et al.*, 1997).

5.3.5 Effect size

The main objective of a meta-analysis is to summarize estimates of the standardized and direct measure of the mean change of a dependent variable (i.e. effect size) in each study. The effect size can also incorporate considerations of sample size (Harrison, 2011). In this study, the effect size was initially either a Pearson product-moment correlation coefficient (r) or Spearman's rank correlation coefficient (rho), that was obtained or estimated from the original study and each of these was transformed to z using Fisher's algorithm (Hedges and Olkin, 1985). Fisher's r/rho-to-z transformation is a variance stabilizing transformation for correlation coefficients with the added benefit of also being an effective normalizing transformation (Fisher, 1921). The Fisher's r/rho-to-z transformed correlation coefficient is equal to

$$z = 0.5\ ln\ ((1+r))/((1-r))$$

One of my aims was to assess the role of spatial grain/plot size in explaining NARR. Many studies reported data conducted at multiple sample plot sizes where, in some cases, these were spatially nested within the same extent (i.e. pseudo-replicates).

Furthermore, some authors had published multiple studies, which could lead to non-independence among studies if particular authors tended to employ particular methodologies that might influence outcomes (i.e. *author effect*). I considered each series of plots of a particular size as a separate dataset, the same approach which has been used in previous meta-analyses (Benayas *et al.*, 2009; Vilá *et al.*, 2011). To deal with the issue of potential pseudo-replication, I ran the analyses and estimated the mean effect size from randomly selected single effect sizes and sample size related ($n = 10000$ permutations) accounting for multiple sample plot size or author effect. I ran the same set of analyses to compare the outcome from a meta-analysis using either Fisher's z transformed correlation coefficient (r) or (rho) as effect size with the full data separately. The mean effect sizes for each of the multiple spatial grains/plot sizes, author effect and Pearson/Spearman correlation coefficient studies were similar to those obtained for all studies and the bias-corrected 95% bootstrap confidence interval (CI) of the whole dataset overlapped the reduced datasets (Appendix M). For this reason, I was confident of including all the data in my analyses. The inclusion of all case studies has been previously used in the amalgamated meta-analysis performed by Vilá *et al.* (2011) to screen for differences in the effect size within levels of ecological complexity. Moreover and for the remaining analyses, I decided to use the Fisher's z transformed Spearman's correlation coefficient (rho) as effect size/response variable, because this non-parametric measure is less sensitive and more robust than Pearson's correlation when the parameters of the joint probability distribution of X and Y are unknown.

In ecological studies, there might be a statistical bias against publishing non-significant results from studies conducted in large sample sizes and studies with small sample sizes. To test for potential biases associated with sample size, I examined standardized effect sizes of the raw data and found that they were slightly negative (rho = -0.07) but not statistically significant correlated to the sample size (P-value = 0.3). This might suggest that studies with small sample sizes are equally likely to be published as large sample sizes when a positive and/or negative NARR is found. To validate this and confirm the absence of a sampling bias (Palmer, 1999), a plot of the effect sizes against the sample size (so-called funnel plot) revealed a funnel-shaped distribution of the data points (Appendix N).

Following Rosenberg (2005), I estimated the fail-safe number, that is, the number of studies that would "nullify" the effect size (i.e. true effect size equal zero) and change the results of the meta-analysis from significant to non-significant. This is 256616 (with target P-values < 0.001). Because this value is larger than 5N + 10 =

975 where N = number of case studies in my dataset, I can affirm that the observed results are a reliable estimate of the true effect. This is also confirmed from a plot of the standardized effect sizes against the normal quantiles. The resulting straight line indicated that the effect sizes are normally distributed (Wang and Bushman, 1998) and this was also tested using the Lilliefors (Kolmogorov-Smirnov) test (see below; Gross, 2012). Overall, the resulting weak publication bias was unlikely to change the meaning of the results (Appendix P).

5.3.6 Meta-regression: multi-model inference approach

To evaluate the role of the selected variables (i.e. moderators) in explaining patterns of NARR, I used multi-model inference within an information-theoretic approach (Burnham and Anderson, 2002) combined with meta-regression analyses. A novel statistical method, multi-model inference analysis in a meta-analysis context, was performed using the *AICcmodavg* package (Mazerolle, 2012) implemented *ad hoc* to deal with meta-regression analysis.

I fitted the meta-analytic random-effects models with moderators via univariate linear (mixed-effects) models to estimate the amount of heterogeneity with a maximum-likelihood estimator. I also fitted multiple regression models (via stepwise selection) to identify moderators that could explain the true effect sizes between all studies when controlling for plot size. This allowed me to partition out plot size more effectively and to make a more direct examination of the influences of the other moderators. The effect size z was used as response variable in all the models and it was normally distributed ($P < 0.01$) using a non-parametric test such as Lilliefors (Kolmogorov-Smirnov) test. Moreover, given that I had no clear *a priori* hypotheses supporting interactions between the explanatory variables considered, I did not include any interaction terms in my model selection procedure. Given that colinearity among moderators can hamper identification of the most causal variables also within an information-theoretic approach, I initially excluded those variables with problems of colinearity (e.g. $rho > 0.5$) and then I calculated a variance inflation factor (VIF) for the set of moderators included in my model selection. As none of the moderators can be considered an indicator of strong colinearity (maximum VIF was 2.5 for mean native species richness; Zuur *et al.*, 2010), I retained all these variables in my multi-model inference procedure and used the Akaike's information criterion to evaluate the relative importance of the moderators (c.f. Murray and Conner, 2009). Moderators were examined to see if they showed a non-linear relationship to the

response by testing for the importance of quadratic terms. None of the moderators showed a significant non-linear relationship with effect size, so I did not include any quadratic terms in the regression models. Problems of missing values in total species richness ($n = 82$ studies) that could bias the results and have a significant effect on the comparisons of models by AICc (see below) led to the exclusion of this variable from the set of moderators. This enabled me to compare models by AICc using complete data cases.

The information-theoretic approach compared the fit of all the possible candidate models (i.e. univariate linear mixed-effects) using Akaike's information criterion corrected for sample size [AICc; *sensu* Burnham and Anderson (2002)]. The difference in AICc values indicates the relative support for the different models. A model is usually considered plausible if its ΔAICc ($AICc_i$ - AICc best-fitting model) is below 4 (Burnham and Anderson, 2002), with the best fitting model (lowest AICc) considered the most plausible.

To quantify the magnitude of the relationship between moderators and the effect size, I also assessed the proportion (%) of total between-study variance explained by the model using an index based on the percent reduction in *true* variance, analogous to the R^2 index used with primary studies. In my case, the R^2 index is equal to

$$R^2 = 1\text{-}\ ((T^2 unexplained)/(T^2 total))$$

where $T^2 total$ is the true variance between-studies variance (T^2) for the full set of studies (intercept only) and $T^2 unexplained$ for the model with the moderators (Borenstein *et al.*, 2009).

5.4 Results

Averaged across all studies, there was a significant positive effect size (NARR transformed into Fisher's $z = 0.26$, $P < 0.001$; Figure 5.1) along with considerable variability in the heterogeneity (Appendix P). The magnitude of the mean effect size varied significantly with the heterogeneity between all studies ($Q_t = 48924.9$, $P < 0.001$). There was a high proportion of observed variation across studies in the effect sizes that is due to heterogeneity rather than chance ($I^2 > 99.6\%$; Appendix P). Across all studies, mean native ($\bar{x}$native $= 241 \pm 140.3$), mean alien ($\bar{x}$alien $= 23 \pm 9.1$) and plot size explained a small (between 4% and 15%) but significant amount of variation in the mean effect size. In particular, the model selection indicated that

the best model always included plot size (i.e. progressive increase in effect size as the plot size increases) while the other models were less plausible (i.e. ΔAICc > 4) in explaining patterns of mean effect sizes (Table 5.1). Although I controlled for plot size, this moderator was still the most plausible in the multiple regression models. When controlling for plot size, the most plausible model fitted mean alien species richness per plot with the overall model that accounted for 17% of the variation. However, this moderator was not statistically significant (i.e. pretending variable *sensu* Burnham and Anderson, 2002). Indeed, adding moderators could explain more variability of effect size but none of the added moderators was statistically significant (Table 5.2).

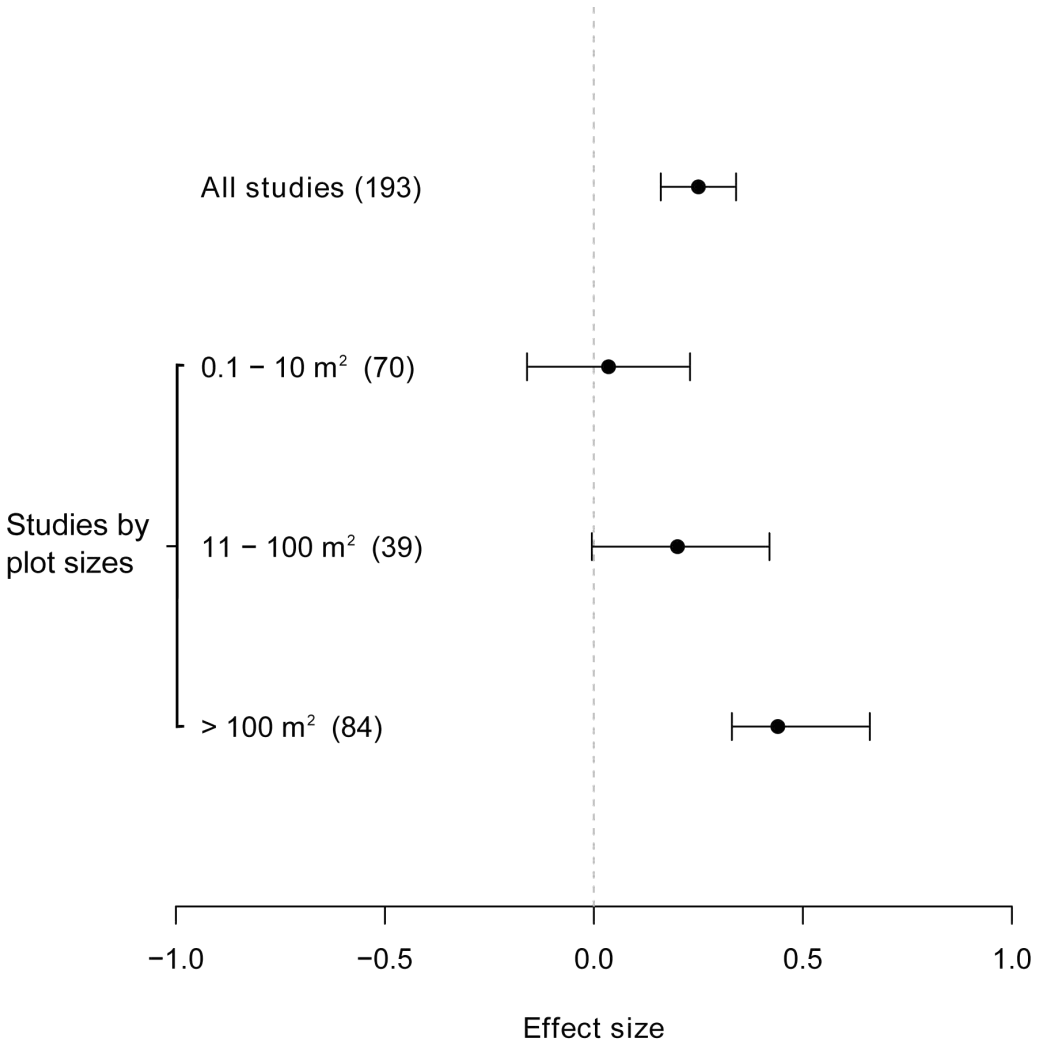

Figure 5.1. Mean effect size (Fisher's z transformation) of the native-alien species richness relationship between all studies and studies divided by different groups of sample grain/plot sizes (see Methods). The bars around the means indicate bias-corrected 95%-bootstrap confidence intervals. A mean effect size is significantly different from zero when its 95% confidence interval do not bracket zero. The sample sizes (i.e. case study) are given next to the bars.

Table 5.1. Results of fitted meta-analytic random-effects models with moderators (i.e. explanatory variables) via linear (mixed-effects) model ranked using the differences in AICc score with the best-fitting model (i.e. ΔAICc) between all studies. For each univariate regression model, parameter estimates of the heterogeneity with maximum-likelihood estimator, bias-corrected 95%-bootstrap confidence intervals and *P*-values are based on permutation test ($n = 10000$). The response variables follow a standard normal distribution (see Methods). Significant variables in a given model are shown in bold. The coefficients of determination (R^2) are also shown.

Levels	Sub-groups	Moderators	d.f.	K	AICc	ΔAICc	Estimate	SE	CI (lb)	CI (ub)	*P*-values	R^2
All studies	-	Plot size	191	3	399	0	**0.042**	0.008	0.026	0.058	< 0.001	**0.15**
		Mean alien	191	3	413	14	**0.109**	0.032	0.045	0.172	< 0.001	**0.06**
		Mean native	191	3	418	19	**0.083**	0.032	0.021	0.145	< 0.05	**0.04**
		Europe	191	3	422	23	-0.029	0.027	-0.082	0.025	n.s.	0.01
		Extent	191	3	422	23	0.023	0.012	0	0.046	n.s.	0.01
		North America	191	3	422	23	-0.199	0.103	-0.401	0.004	n.s.	0.01
		Grassland	191	3	422	23	-0.224	0.117	-0.454	0.007	n.s.	0.01
		ANR	191	3	424	25	0.027	0.039	-0.051	0.104	n.s.	0.01
		N° plots	191	3	425	26	-0.027	0.027	-0.081	0.027	n.s.	0.01
		Forest	191	3	425	26	0.114	0.129	-0.141	0.371	n.s.	0.01
		Islands	191	3	425	26	0.187	0.238	-0.282	0.657	n.s.	0.01
		Mainlands	191	3	425	26	-0.187	0.238	-0.657	0.282	n.s.	0.01
		N° habitats	191	3	425	27	0.028	0.052	-0.074	0.131	n.s.	0.01
		Riparian	191	3	425	27	0.081	0.183	-0.281	0.442	n.s.	0.01

Table 5.2. Results of fitted meta-analytic random-effects models with moderators (i.e. explanatory variables) via multiple regression models and stepwise selection ranked using the differences in AICc score with the best-fitting model (i.e. ΔAICc) between all studies. For each model, parameter estimates of the heterogeneity with maximum-likelihood estimator, bias-corrected 95%-bootstrap confidence intervals and *P*-values are based on permutation test ($n = 10000$). The response variables follow a standard normal distribution (see Methods). Significant variables in a given model are shown in bold. The coefficients of determination (R^2) are also shown. I might mention here the fact that the model with a unique predictor (i.e. plot size) has only moderate plausibility.

Levels	Sub-groups	Moderators	d.f.	K	AICc	ΔAICc	Estimate	SE	CI (lb)	CI (ub)	*P*-values	R^2
		Plot size***	190	4	396	0	**0.037**	0.009	0.020	0.054	< 0.001	**0.17**
		+ Mean alien	-	-	-	-	0.063	0.034	-0.004	0.130	n.s.	
		Plot size***	189	5	397	0.89	**0.041**	0.009	0.023	0.059	< 0.001	**0.16**
		+ Mean alien	-	-	-	-	**0.087**	0.041	-0.007	0.168	n.s.	
		+ Mean native	-	-	-	-	**-0.046**	0.043	-0.130	0.039	n.s.	
		Plot size***	189	5	397	1.09	**0.039**	0.009	0.022	0.056	< 0.001	**0.16**
		+ Mean alien	-	-	-	-	0.052	0.036	-0.019	0.122	n.s.	
		+ N plots	-	-	-	-	-0.026	0.027	-0.079	0.027	n.s.	
		Plot size***	190	4	397	1.21	**0.047**	0.009	0.030	0.064	< 0.001	**0.16**
		+ N habitats	-	-	-	-	-0.079	0.052	-0.182	0.025	n.s.	
		Plot size***	190	4	397	1.21	**0.043**	0.008	0.027	0.059	< 0.001	**0.15**
All studies	**-**	+ N plots	-	-	-	-	-0.039	0.026	-0.089	0.012	n.s.	
		Plot size***	191	3	398	1.52	**0.042**	0.008	0.026	0.058	< 0.001	**0.15**
		Plot size***	188	6	398	2.02	**0.042**	0.009	0.024	0.061	< 0.001	**0.15**
		+ Mean alien	-	-	-	-	0.076	0.043	-0.008	0.160	n.s.	
		+ Mean native	-	-	-	-	-0.045	0.043	-0.129	0.039	n.s.	
		+ N plots	-	-	-	-	-0.026	0.027	-0.079	0.027	n.s.	
		Plot size***	187	7	399	3.18	**0.045**	0.010	0.026	0.064	< 0.001	**0.15**
		+ Mean alien	-	-	-	-	0.073	0.043	-0.012	0.157	n.s.	
		+ Mean native	-	-	-	-	-0.036	0.044	0.408	-0.122	n.s.	
		+ N plots	-	-	-	-	-0.018	0.028	0.525	-0.074	n.s.	
		+ N habitats	-	-	-	-	-0.054	0.056	0.338	-0.164	n.s.	
		Plot size***	190	4	400	3.58	**0.041**	0.009	0.023	0.060	< 0.001	**0.15**
		+ Mean native	-	-	-	-	0.005	0.036	-0.065	0.076	n.s.	

For studies sub-grouped by plot sizes (0.1 - 10, 11 - 100, and > 100 m^2), the magnitude of the mean effect size varied significantly with the heterogeneity between studies divided by plot sizes (Q_t ranging from 5761.6 to 20678, $P < 0.001$) with the 95% confidence interval of the mean effect size overlapping zero only in those ≤ 100 m^2 ($n = 109$; Figure 5.1 and Appendix P). For plot size < 10 m^2, the mean effect size (i.e. NARR transformed) was neither significantly positive nor negative, but close to zero. For studies with plot size between 11 and 100 m^2, the mean effect size is greater than zero but not statistically significant. This may be also due to heterogeneity in the sign of NARR found at this spatial grain/extent (Appendix O). For studies with plot size > 100 m^2 the mean effect size was instead significantly positive.

For studies sub-grouped by plot size with plot size < 10m^2, there was a consistent but not significant positive relationship between moderators and the mean effect size. For studies which used plot sizes between 11 and 100 m^2, plot size and number of plots explained the variation in the effect size (Table 5.3). For those with plot size > 100 m^2, plot size, mean alien species richness per plot and ANR explained the variation in the effect size. While the best models consistently included plot size, the other variables noted above were not statistically plausible. Furthermore, for the remaining variables, which were hypothesized to be related to effect size, the 95% confidence interval of the parameter estimates overlapped zero. Therefore, the results could not support the hypothesis that these explanatory variables could explain significant variation in NARR when plots were grouped by plot size class. In studies which used plot sizes between 11 and 100 m^2, only plot size was positive, accounting for 29% of the variation, while the number of plots was slightly significant ($P < 0.05$) but not statistically plausible (ΔAICc $= 9.6$). For studies with plot size > 100 m^2, plot size explained a small but significant amount of variation (variation accounted for 19%) while mean alien richness and ANR explained respectively 9% and 5% of the variation, but these also lack of statistical plausibility (Table 5.3).

Table 5.3. Results of fitted meta-analytic random-effects models with moderators (i.e. explanatory variables) via linear (mixed-effects) model ranked using the differences in AICc score with the best-fitting model (i.e. ΔAICc) between studies sub-grouped by different sample plot sizes (see Methods). For each univariate regression model, parameter estimates of the heterogeneity with maximum-likelihood estimator, bias-corrected 95%-bootstrap confidence intervals and *P*-values are based on permutation test ($n = 10000$). The response variables follow a standard normal distribution (see Methods). Significant variables in a given model are shown in bold. The coefficients of determination (R^2) are also shown.

Levels	Sub-groups	Moderators	d.f.	K	AICc	ΔAICc	Estimate	SE	CI (lb)	CI (ub)	*P*-values	R^2
Studies by plot size	0.1 - 10 m^2	Plot size	68	3	165	0	0.123	0.071	-0.016	0.262	n.s.	0.06
		Mean native	68	3	167	2.5	0.084	0.091	-0.099	0.266	n.s.	0.02
		Mean alien	68	3	168	2.8	0.053	0.071	-0.086	0.191	n.s.	0.01
		N° plots	68	3	168	3	0.022	0.049	-0.076	0.119	n.s.	0.01
		ANR	68	3	168	3	0.005	0.074	-0.144	0.153	n.s.	0.01
	11 - 100 m^2	Plot size	37	3	76.9	0	**0.524**	0.134	0.253	0.795	< 0.001	**0.29**
		N° plots	37	3	86.4	9.6	**-0.112**	0.052	-0.217	-0.007	< 0.05	**0.08**
		N° habitats	37	3	89.2	12.4	-0.171	0.123	-0.421	0.079	n.s.	0.05
		Extent	37	3	89.4	12.5	0.035	0.026	-0.018	0.089	n.s.	0.01
		Mean alien	37	3	91	14.1	0.051	0.091	-0.133	0.235	n.s.	0.01
	> 100 m^2	Plot size	82	3	154	0	**0.046**	0.012	0.022	0.071	< 0.001	**0.19**
		Mean alien	82	3	161	5.1	**0.105**	0.039	0.027	0.183	< 0.05	**0.09**
		ANR	82	3	163	7.8	**0.116**	0.051	0.014	0.218	< 0.05	**0.05**
		Extent	82	3	166	12.2	0.004	0.014	-0.031	0.038	n.s.	0.01
		N° habitats	82	3	166	13.6	-0.026	0.087	-0.198	0.147	n.s.	0.01

With regard to such moderators as different habitat types (number of studies in grassland = 50, forest = 37, riparian = 17), ecosystems (islands = 11, mainlands = 182) and biogeographic regions (Europe = 43, North America = 115), there were no significant differences in the consistent mean positive NARR between studies (Figure 5.2). Testing of invasion rates (i.e. mean alien richness and ANR) in these three habitat types, in ecosystems and in regions revealed no significant differences.

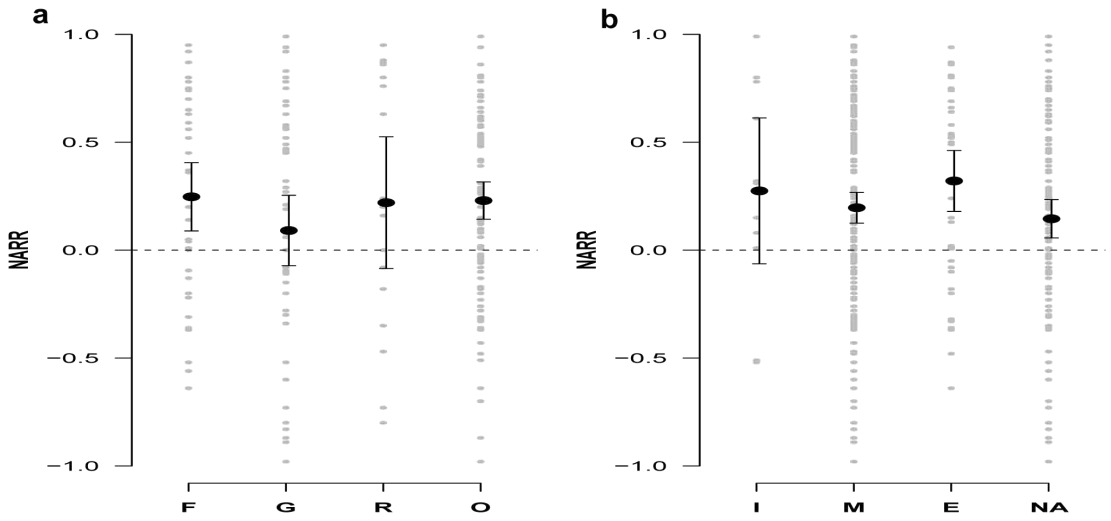

Figure 5.2. The mean and bias-corrected 95%-bootstrap confidence intervals for the NARR for (a) four habitats (F = Forest, G = Grassland, R = Riparian, O = Others) and (b) ecosystems and biogeographical areas (I = Islands, M = Mainlands, E = Europe, NA = North America). Grey points are individual case study. The horizontal dotted line shows value of NARR = 0.

5.5 Discussion

Generalizations about NARR have been slow to develop (Stohlgren *et al.*, 2002, 2006) although previous reviews of published data observed that this relationship is scale dependent (Herben *et al.*, 2004; Fridley *et al.*, 2007). My study confirms that across a broad range of spatial grains/plot sizes and extents worldwide, NARR becomes increasingly positive and significant as plot size increases (Figure 5.1; see also Herben *et al.*, 2004; Stohlgren *et al.*, 2006; Fridley *et al.*, 2007). My global scale study confirms that plot size explained the largest amount of variation in the mean effect size, with a trend of increasingly positive values for NARR as plot size increases (Table 5.1 and Table 5.2).

At large plot sizes a significant positive NARR is found because observational studies are often collected at progressively larger areas where there is an increasing

heterogeneity in resources with a net increase in native species richness and a greater invasion of species-rich habitats (Levine and D'Antonio, 1999; Stohlgren *et al.*, 2002, 2003a; Davies *et al.*, 2005). At large spatial grain and extent where there is greater spatial heterogeneity of environmental conditions (i.e. abiotic factors), a positive NARR results and it may be the case that the biotic acceptance hypothesis offers some explanation (Stohlgren *et al.*, 2003b; Davies *et al.*, 2005; Gilbert and Lechowicz, 2005; Stohlgren *et al.*, 2006).

While a significant positive NARR is found at large spatial grains/plot sizes (> 100 m^2), my results are in contrast with several previous studies [see Fridley *et al.* (2007) and reference therein] and show an overall pattern of positive but non-significant NARR at small spatial grains/plot sizes (< 100 m^2). At very small spatial grains/plot sizes, a statistical artefact related to individual species size (i.e. constraint of the numbers of individuals species when sampling units are very small) may affect NARR (Fridley *et al.*, 2004; Herben *et al.*, 2004; Fridley *et al.*, 2007). Stohlgren *et al.* (2006) highlighted that "fine-scale negative relationships may be, in fact, the result of this statistical artefact rather than niche-based processes". At small spatial grains/plot sizes, competition for available resources and resistance to invasions in species-rich communities, where high diversity results in less invaded ecosystems because the ecosystems are saturated and all niches are filled, may lead to the biotic resistance frequently resulting in negative NARR (Fridley *et al.*, 2007; Bartomeus *et al.*, 2012). In my case, this positive NARR may be ascribable to the fact that 77% (84 out of 109) studies at small spatial scales (< 100 m^2) were conducted in disturbed habitats (e.g. grassland or riparian) where, as shown in Chapter 3 and Chapter 4, the positive NARR are more likely to occur. Habitats characterized by highly intense levels of disturbance (natural or anthropogenic, e.g. flooding, burning or livestock grazing and fertiliser addition) may favour the introduction and the spread of alien species allowing these disturbed habitats to be invaded by other alien species. This may lead to higher alien species richness than native species richness and consequently to a positive NARR.

Agreement on the relationship between native and alien richness may be difficult to reach as findings at different spatial scales are contradictory. Although not evident from my results, one might speculate that this critical difference in NARR between small and large sample plot sizes may be due to variation in community size (i.e. studies employing small plot size may tend to sample more homogenous vegetation and environments while studies with large plot size tend to sample a wider area and consequently find greater variation in community composition and environmental

heterogeneity). Furthermore, and this is widely accepted in the scientific literature (Stohlgren *et al.*, 2006; Fridley *et al.*, 2007; Bartomeus *et al.*, 2012), it may also be the case that the biotic resistance and biotic acceptance hypotheses are useful in explaining the changing sign of NARR between small and large sample plot sizes. In addition, the "Niche Differentiation Hypothesis" (MacArthur and Levins, 1967) and the "Habitat Filtering Hypothesis" (Keddy, 1992) might also play a role in explaining the variation of NARR. The "Niche Differentiation Hypothesis" with limiting similarity (Pacala and Tilman, 1994; Chesson, 2000) may be involved in the negative NARR due to more niche space that is filled by native species resulting in saturated ecosystem where less alien species can invade it. The "Habitat Filtering Hypothesis" may instead limit both native and alien species occurrence with both species exhibiting similar traits (Marini *et al.*, 2012), and this may lead to a positive NARR at large spatial grains and extents (Gross *et al.*, 2013).

If NARR is scale dependent, are there any moderators that may explain the variability in NARR worldwide when plot size is controlled? Plot size explained the largest amount of variation in the mean effect size. When I controlled for plot size (Table 5.2), this moderator was still found to be plausible in the multiple regression models. These findings allowed me to point out the extreme scale dependency of NARR. This was also evident across all studies and, when grouped by plot size, for those with plots >10 m^2, but not for smaller plot sizes (Figure 5.1). Shea and Chesson (2002) proposed to reconcile both biotic resistance and biotic acceptance hypotheses introducing the spatial scale as covarying factor in the NARR along environmental gradients. Some ecosystems, they argue, may allocate more or less species because, for instance, there is less or more competition. Where the number of both native and alien species is high this leads to a positive NARR; conversely, where the number of both is lower a negative NARR may result. Shea and Chesson (2002) concluded that NARR is heavily influenced by additional covarying effects related to spatial heterogeneity which become more important as plot size increases. This is confirmed by the literature. Similar factors associated with native species also increase with extent, such as habitat heterogeneity, environmental gradients, and increased likelihood of encountering disturbed habitats. These factors, possibly along with biotic acceptance, may also be responsible for the richness of native species and the increasing establishment of alien plant species as the spatial grain/plot size of observation is increased (> 100 m^2). This results in a consistent positive NARR (Stohlgren *et al.*, 1999, 2001, 2002, 2003a, 2006). However, without changing spatial grain (i.e. keeping within same plot size), habitat heterogeneity combined with high

resource availability (e.g. energy/water/nutrients; Bashkin *et al.*, 2003; Stohlgren *et al.*, 2005; Fridley, 2011) and disturbance (Fox and Fox, 1986) may promote the coexistence of native and alien species (i.e. increasing both number of species) and consequently determine a positive NARR (Stohlgren *et al.*, 2006). However, although less habitat heterogeneity within small plot size (< 100 m^2) may be encountered, this may still vary to an extent, NARR shifting from positive to negative as heterogeneity decreases as Fridley *et al.* (2007) has highlighted. This is confirmed in my study although with a lack of consistency and plausibility (Table 5.3).

In addition to plot size, the literature suggests that mean native and mean alien species richness per plot is likely to be a significant factor in explaining NARR (Levine and D'Antonio, 1999). In Chapter 3 and Chapter 4, I have shown how in the heterogeneous landscape of Banks Peninsula the vegetation structure and the species communities related (where mean native and alien species richness per plot differ depending on the different species communities) determined the change in the sign of NARR along an elevational gradient. One might assume that this result would be confirmed at the global scale. However, for reasons that are not entirely clear, the global meta-analysis showed that, while mean species richness is in fact a predictor of some significance of NARR, it presents only limited statistical plausibility (Table 5.1 and Table 5.2 and Table 5.3).

I found that another possible predictor of NARR is the measure of the level of invasions (ANR). However, the significant positive relationship between ANR and NARR (Appendix O) is marked by a reduced statistical plausibility (Table 5.1 and Table 5.3). These findings make it hard to advance a satisfactory explanation of NARR. It may be the case that increasing positive NARR are related to increasing levels of invasion. ANR is facilitated by environmental disturbance and increasing habitat suitability for alien species and also by increased propagule pressure (e.g. increasing intentional and unintentional transport and release of seeds and propagules; Hobbs and Huenneke, 1992; Levine *et al.*, 2004; Pyšek and Hulme, 2005) leading to a positive NARR. This finding agrees with Bartomeus *et al.* (2012), who highlighted the importance of human-related factors which may not only provide novel niche opportunities but also increase propagule pressure. A variety of human-related factors (e.g. human settlements, land-use history and management; Lockwood and McKinney, 2001; Parker *et al.*, 2010; Boughton *et al.*, 2011) and see Chapter 4, may alter competition regimes and plant communities assemblage to facilitate the invasion of both native and alien plant species that may produce a positive NARR. However, histories of propagule pressure in observational studies reporting positive NARR are

often difficult to determine (Stohlgren *et al.*, 2006). In my study it was difficult to quantify the levels of human-related disturbance because they were significantly correlated with the extent of the study ($rho = 0.21$, $P < 0.001$). The larger the extent of the study is the higher the chance that disturbance occurs. At larger extent it is difficult to disentangle human-related and environmental factors because these may be entwined. Difficulties in accurately measuring propagule pressure in plants (Lockwood *et al.*, 2005) make it also harder to successfully resolve the invasion paradox.

My results regarding different habitat types (e.g. grasslands, forests and riparian zones), ecosystems (e.g. islands and mainlands) and biogeographic regions (e.g. Europe and North America) show that in none of them can any significant difference in the sign of NARR be detected (Figure 5.2). However and consistent with the findings of Martin *et al.* (2008), my results highlight that forests around the world have a significant positive NARR (Figure 5.2). Initially we may think of attributing this to high invasion rates (i.e. high number of alien species and high ANR), but the results in my study do not confirm this hypothesis. In riparian zones, Stohlgren *et al.* (1998) found a slightly significant negative NARR. However, my results show that there is a positive NARR in these habitats worldwide, but no satisfactory explanation can be advanced because it is not clear whether those positive findings are due to increased disturbance (i.e. flooding; Planty-Tabacchi *et al.*, 1996; Tabacchi and Planty-Tabacchi, 2005), increased resource availability (Stohlgren *et al.*, 1998), higher soil fertility and pH (Maskell *et al.*, 2006) or higher turnover of plants (Stohlgren, 2002). Therefore, further study to determine causal mechanisms of all these patterns is needed.

5.6 Conclusion

The overall positive NARR worldwide is scale dependent, as my study, has shown over both variable plot sizes (i.e. all studies) and controlled sub-groups of less variable plot sizes. It may be noted that almost all positive NARR patterns documented so far have been reported in developed countries, where human impact on both native and alien flora is usually high (Bartomeus *et al.*, 2012). Ecologists have long been searching for a general theory of community invasibility and if this is to be realized, further investigation of NARR is required worldwide. It is essential for purposes of conservation that seek to prioritize areas for invasive alien species control

and prevention to focus our attention and efforts in habitats where the levels of community invasibility are high and significant (e.g. forests and riparian zones) but also on protecting native communities that are still intact (e.g. Firn *et al.*, 2008). Future investigations of species richness on islands will further develop a quantitative approach to better understand the processes that govern NARR worldwide.

Chapter 6

Conclusion

6.1 Thesis aims

Questions about the relationship between native and alien species diversity, and the factors controlling this, have been widely discussed in the literature but there is no clear consensus around whether relationships are positive or negative and what the underlying mechanisms are. One of the aims of my thesis was to identify and quantify the relative importance of abiotic and biotic factors that covary with dominant environmental gradients and underpin native and alien plant communities richness patterns and determine how these factors characterize native and alien species composition and structure on local-regional scale. A key contribution of this thesis is to show that, across a heterogeneous environment such as Banks Peninsula, both positive and negative relationships between native and alien species richness can arise at local species community scale (Chapter 3) and at regional landscape-scale (Chapter 4), with this outcome moderated by the effects of land-use history and management. Another aim of my thesis was to identify, quantify and analyse the relative importance of factors that may explain the variability of native and alien species richness relationship (NARR) at global scale. This is developed in Chapter 5.

6.2 What do the findings mean for the broader field of invasion ecology?

6.2.1 Land-use history and management: effects on species community structure and patterns

My study confirms a growing and recent body of evidence (Parker *et al.*, 2010; Boughton *et al.*, 2011) that indicates that (1) species composition and structure and the degree of biotic homogenization and nestedness and (2) species richness patterns and consequently the sign and magnitude of NARR may be more strongly shaped by land-use history and management than by climate along elevational gradients.

Land-use history and management, firstly, and climate, secondly, both of which covary with elevational gradients, have been found to determine distinct native and alien species communities, where native species communities that grow at high-elevations are more resistant to invasion by alien species while low- to mid-elevation alien species communities are favoured in their distribution and dominance by human-related disturbances. These findings are similar to those of other studies (Wil-

son, 1989; Wilson *et al.*, 1989; Oneal and Rotenberry, 2008; Brown and Boutin, 2009; Otýpková *et al.*, 2011) where native and alien species communities differed spatially and ecologically and are differently related to human-related and environmental factors. At the local-regional scale of Banks Peninsula, land-use history and management are in fact responsible for the shift from alien grassland communities to remnant or regenerating native forest and shrubland. This reflects into positive or negative native-alien species richness relationships that occur in community types that are dominated by alien species (positive NARR) and in community types dominated by native species (negative NARR; Chapter 3). In alien dominated communities, which are composed mostly of alien pasture grasses and herbs, land-use and -management determine the species composition allowing pastures, for example, to be invaded by other alien and native species leading to a positive NARR. Native dominated communities, mainly remnant or regenerating native woody vegetation, may be less susceptible to invasion by alien grass or herbaceous species better adapted to more open environments and this leads to a negative NARR (see also Chapter 4). It is clear therefore that human-related factors or proxy measures (e.g. land-use history and management) must be taken into account when studying structure and pattern of native and alien species communities at local-regional scales.

One of the novel approaches of my study was to compare the degree of biotic homogenization by alien species of native species community composition in habitat types with different regimes and intensity of human-related disturbances along elevational gradients. The findings that native dominated communities are less homogenized than the other communities (Chapter 3) follows what Mack (1989) found. In fact, the interactions of human-related disturbances (e.g. fire, grazing and agriculture) together with propagule pressure are likely to homogenize the composition of the flora where burning and grazing are considered major and historical disturbances of plant communities not only in the Banks Peninsula flora but also in the New Zealand flora (Mark, 1965; Buchanan, 1968; Scott *et al.*, 1988; Calder *et al.*, 1992; Yeates and Lee, 1997; Mark and Dickinson, 2003; Ewans, 2004; Espie and Barratt, 2006). Looking at the literature, several studies have found contradictory results: for example, in a study of a regenerating forest in North America, Brown and Boutin (2009) found that direct measures of recent human-related disturbance (i.e. roads, selective cuttings) did not influence community composition, while historical land-use (past clearance or past grazing) influenced native and alien species richness. In a more recent study, Otýpková *et al.* (2011) showed that in a mountain region of the Czech Republic, native and alien species

richness was associated with different environmental factors (e.g. land-use types) but these were not associated with species composition. Consequently, the implications of this for restoration ecology mean that land managers and decision makers wanting to determine where alien species most likely will need to be controlled will have to consider areas where land-use history and management may be marked (Diez *et al.*, 2009a; Boughton *et al.*, 2011).

As my study found and others agree, alien species are more common in areas with a higher degree of human-related disturbance, and less common in areas of semi-natural condition (McKinney, 2004, 2006; Lososová *et al.*, 2012). For biological conservation purposes, the latter areas should be considered of greater importance where the preservation of native species biodiversity must be emphasized (McKinney, 2006) because, although biotic homogenization may be less marked and significant than other areas, it may become a more serious problem where natural or human-related disturbances occur.

What about species richness relationship patterns? My thesis highlights that agreement to date about the mechanisms underlying native and alien species richness relationship is not clear. The consensus whether relationships are positive or negative suffers from the fact that the spatial grain and extent of studies are rarely independent and that the grain size covaries with the spatial extent examined (Hulme, 2008). In addition, the shift from biotic to abiotic factors also potentially drives the sign and magnitude of NARR with increasing spatial grain and extent (Fridley *et al.*, 2007). NARR may be driven by different factors depending on the plot size used in the study: (1) at small plot size (e.g. < 10 m^2), biotic factors (e.g. community composition) may act as primary drivers; (2) at medium plot size (e.g. 11 - 100 m^2), land-use and -management may be the main drivers; and (3) at large plot size (e.g. > 100 m^2), climate can be considered the main driver. Bearing this in mind, I found that the effect of land-use history and management, which covaries with climate along elevational gradients, moderates both positive and negative species relationships across a heterogeneous environment such as Banks Peninsula. In fact, both positive and negative NARR can occur within the same plot size and across the same landscape, depending on the plant community and the underlying gradients (i.e. human and environmental) examined (Chapter 3 and Chapter 4). Positive and negative NARR respectively have been also found in other studies that used similar plot size as the one on Banks Peninsula and where the landscape was recently subjected to the establishment of agriculture practices [e.g. grazing, fertilization, sowing of alien species; McIntyre and Lavorel (1994)] or along a sub-alpine gradient

where grazing activities had been abandoned for over 30 years with a resulting semi-natural landscape status nowadays (Godfree *et al.*, 2004).

Another contribution of my study to the field of invasion ecology is the fact that NARR is correlated to the level of invasion [alien to native species richness ratio namely ANR; Lonsdale (1999); Chown *et al.* (2005); Hulme (2008); Marini *et al.* (2009)] although it has reduced statistical plausibility (see Chapter 5). My study found that at local species community scale, ANR decreases across community types going from a mean value of 6.8 in alien dominated communities to 0.2 in native dominated community (see Chapter 3). At regional landscape-scale, there is a higher value of ANR than globally (ANR = 2.1 and 0.62 respectively). At local-regional scale, these results may be attributed (1) to the distinct native and alien plant communities that grow along the strong elevational gradients of the Peninsula; and (2) to the marked human-related gradients (i.e. land-use and -management) that covary with environmental gradients (i.e. climate and elevation) across the Peninsula and determine native and alien species composition and structure and richness patterns. Areas characterised by highly intense levels of land-management (e.g. burning, livestock grazing, fertiliser addition) may favour the introduction and the oversowing of alien pasture species allowing pastures to be invaded by other alien species. This may lead to higher alien species richness than native species richness (these species have been also probably removed) and consequently high values of ANR. In areas where land is less intensively managed, the remnant or regenerating native woody vegetation may be less susceptible to invasion by alien grass or herbaceous species better adapted to more open environments, thus leading to low values of ANR. As described previously, these two main drivers are linked together, the high (or low) human-related factors and high (or low) related impacts drive the native (or alien) plant species communities and their composition and richness patterns where the establishment and invasion by alien species may lead to high levels of invasion resulting in a potential homogenization effect of native communities.

Although the important role of human-related disturbance is confirmed in my study on Banks Peninsula, where a strong human-related gradient affects species composition and structure and richness patterns and consequently NARR, I agree with Fridley (2011) that human-related disturbance can be seen as a strong but not unique driver of variation in community invasibility. Alien species invasion may also be observed in relatively undisturbed ecosystems where resource availability (e.g. water, light and nutrients) may play a key role (Fridley, 2011).

6.3 What are some of the limitations of the studies conducted?

6.3.1 Sampling methods: time and cost are significant limitations

An important element when studying species structure and patterns in relation to the spatial distribution of environmental predictors is designing an efficient sampling method to achieve a representative sample of the population (Hirzel and Guisan, 2002; Rew *et al.*, 2006) and to capture the environment (Neldner *et al.*, 1995). Obviously, a range of different sampling methods are available and they can be used [see Hirzel and Guisan (2002); Rew *et al.* (2006); Maxwell *et al.* (2012)]. In my study, the 36 m^2 plot size is consistent with recommendations for adequately sampling grassland vegetation in New Zealand (Hurst and Allen, 2007) and Europe (Chytrý and Otýpková, 2003; Otýpková and Chytrý, 2006). The Banks Peninsula systematic sampling method (Wilson, 1992) is similar to the Braun-Blanquet relevé methods that are widely used for phytosociological studies (Mueller-Dombois and Ellenberg, 1974) and to the Recce description method that was initially designed for surveying of mountain forests (Allen, 1992) but it is now the most widely used method for collecting diverse plant species communities composition and structure in New Zealand natural and managed habitats (Hurst and Allen, 2007). In Chapter 2, I assessed the accuracy of different sampling schemes and determined that the 1983-1988 systematic floristic survey (Wilson, 1992) had reliably sampled the Peninsula environments although with (1) some sampling limitations (e.g. detecting fewer population density areas and in areas near rivers or undersampling in forest), (2) statistical limitations [i.e. systematic sampling can reduce the degrees of spatial autocorrelation (Smith, 1994), but it does not exclude the independence of errors (Green, 1979); see also Higgins *et al.* (1999)] and (3) although accurate, this systematic method can be time consuming to complete (i.e. 5 years) with significant costs involved.

At this point, a question can be raised: would I suggest conducting a future floristic survey of Banks Peninsula using the same sampling methods to better study species community composition and structure and richness patterns? The systematic sampling method worked well in giving significant results for Banks Peninsula, but this method may not be recommended if the aims are a straightforward floristic survey in this study area or in one with similar extent and also characterized by a

heterogeneous landscape with marked human-driven habitats. But other sampling methods may be preferred, for example, the random or systematic Recce description method (Hurst and Allen, 2007) that collect semi-quantitative vegetation data with the aim to understand vegetation-environment relationship using the site description and stand parameters (e.g. topographic data and ground surface and cover) and vegetation description (e.g. structure and composition and occurrence of the plant species communities) at different spatial grains/plot size depending on the sampled habitats (i.e. 2 m^2, 20 - 50 m^2, 80 - 150 m^2 and 200 - 400 m^2 in turf, grassland, shrubland and forest respectively). Moreover, the Modified-Whittaker nested vegetation sampling method (Stohlgren *et al.*, 1995) can also be used which may allow for better estimates of native and alien species composition and structure and the analysis of both species richness at multiple spatial grains/plot size (i.e. 1 m^2, 10 m^2, 100 m^2 and 1000 m^2) in natural (i.e. forest versus grassland) and managed (i.e. grazed versus ungrazed) habitats.

To detect species presence/absence and abundance of plant invasions, grid and random points, and targeted (i.e. stratified continuous) or random transects provide the most consistent sample of the vegetation (Rew *et al.*, 2006). Moreover, roadside sampling methods are also commonly used in phytosociological studies for providing species composition and abundance. However, when the landscape is highly managed, such as Banks Peninsula, plant species detection can be difficult as the native and alien plant species are distributed non-homogeneously and in irregular patches across the landscape (Maxwell *et al.*, 2012). In these circumstances, roadside or non-adaptive transect sampling methods are efficient in time and performance, but only for species with restricted distribution [e.g. along the roads; Maxwell *et al.* (2012)]. When plant species populations are patchier and dispersed, like alien plant species at early and later stages of invasion, the adaptive cluster sampling methods *sensu* Thompson and Higgins (2002) generally proved to be the most time-efficient and effective in detecting plant species (Thompson, 2006). Adaptive survey sampling methods (i.e. where sampling units are added to the fixed initial sample units if alien plant species are observed or if the magnitude of the variable of interest satisfies a specific condition) may provide unbiased sampling for best estimates of distribution of rare and spatially clustered population of native (or alien) plant species (Maxwell *et al.*, 2012). A limitation to this approach lies on the fact that the use of adaptive cluster sampling methods has only been recently discovered for surveying alien plant species and it requires good computational effort.

6.3.2 Data availability, direct measurement and spatial resolution of layers

The availability or the direct measurement of several variables, especially human-related factors, may add, as in my case study, further explanatory power to the statistical model used and deepen our understanding of drivers affecting native (and/or alien) plant species distribution in a landscape that is as marked by land-use history and management as Banks Peninsula. For example, data on fire frequency, which was available to Foxcroft *et al.* (2004) in a study in South Africa and which increased the accuracy of their model, was not available for Banks Peninsula.

Another major limitation was that the human-related gradient (i.e. land-use history and management) was not directly measured but inferred from the analysis of vegetation pattern using ordination and classification techniques rather than assessed independently. This factor was similarly inferred but not measured by Wiser and Buxton (2008) in order to explain the invasion process of local plant community on Banks Peninsula. Our understanding, generally, of community composition and structure may be enhanced if further data (e.g. land-use changes, fire frequency, records of grazing) could be directly measured. The importance of land-use and -management would be much stronger if an independent assessment of these drivers could be made. But, as highlighted in Chapter 4, land-use history and management and related impacts (e.g. land clearance, grazing) may be less discernible at larger grain sizes (> 1 km^2) where other broad-scale abiotic factors (e.g. climate and geology) are more likely to shape species structure and patterns.

Similar outcomes to mine (see Chapter 3 and Chapter 4) were found in a previous study of the modified landscape of Banks Peninsula which showed that plant species communities on montane outcrops (i.e. native and alien plant species growing at elevations $>$ 500 m a.s.l.) are strongly spatially segregated (Wiser and Buxton, 2009) and the native plant community has been homogenized by alien species (Wiser and Buxton, 2008). This geographic distinction of native and alien plant communities can be attributed, as in my study across the entire Banks Peninsula, to climate factors that covary along elevational gradients and where the levels of human-related disturbances determine an invasion gradient. In addition, Wiser and Buxton (2009) found that other factors, for example soil pH, added explanatory power to an understanding of the distinctiveness of the species community. In my case, this measure was not statistically significant in explaining either native or alien species composition (Chapter 3) but, for reasons which are not entirely clear, it was

significant for the variation in their species richness (Chapter 4). These findings may be limited because of differences in the spatial grain/plot size of sampling: for example Wiser and Buxton (2009) sampled the soil pH directly across the area while I used a verified polygon layer at greater scale (i.e. 1:63000/1:50000). Regarding the geology, QMAP data (GNS Science) was available but instead I used a geological map (Institute of Geological and Nuclear Sciences 1983, scale 1:100000) to produce a classification of the lithological conditions on Banks Peninsula. Although this data has a finer resolution than the QMAP (i.e. 1:250000) I did not include it in the final Banks Peninsula geodatabase because of its colinearity with mean soil pH ($rho > 0.5$). Differences between the findings of Wiser and Buxton (2009) and my study may be also due to the different statistical techniques used. Wiser and Buxton (2009) used a hierarchical multiple regression linear model [namely HLM; Raudenbush (2002)] while I used a generalised least-squares model [namely GLS; Legendre (1993); Dormann *et al.* (2007)]. HLM is considered the most appropriate when taking into account the important issue of clustering of data within groups (e.g. rare species within native and alien community types) to study the importance of human-related disturbance in affecting species communities [e.g. native and alien species; Wiser and Buxton (2009)]. GLS is instead a linear model that allows the variances of the observations to be unequal (i.e. heteroscedasticity) or to have a certain degree of correlation (e.g. spatial autocorrelation) between the observations. GLS directly models the spatial covariance structure in the variance-covariance matrix (Dormann *et al.*, 2007; Pinheiro and Bates, 2009) and it can be used efficiently when studying species patterns derived from data points (i.e. plots) as in my case study.

Spatial resolution of layers may be also a limiting factor as spatial scale is important to both species distribution and related environments (Elith and Leathwick, 2009). When studying their relationship, it is important that the grain (i.e. grid cell or polygon size) of the explanatory variables is consistent with the species data layers (Elith and Leathwick, 2009). However, in most cases around the world, as in Banks Peninsula, this kind of consistency is difficult to find. Although I verified the accuracy of the available data, I was unable to match the spatial grain of species and environmental predictor data. It is possible that using finer resolutions for sampling schemes or the underlying data may improve the understanding of drivers in explaining species distribution patterns as it shown by Keil *et al.* (2012).

The design of an efficient sampling strategy and the availability of further data (e.g. fire frequency, nutrient values or direct measures of human-related factors) along with the spatial scale of explanatory variables that is consistent with the

species data layers may be useful in improving the accuracy of any statistical model attempting to explain species structure and patterns. As scientists we have to work on the data we have and the accuracy we get is always a reflection of this.

6.4 Are the results likely to have broad application in other systems?

6.4.1 Conservation programs after agriculture abandonment

According to the general theory of community resilience in relation to levels of invasion/disturbance, the relative stability of a species community *sensu* Sutherland (1974) is characterized by its resistance (i.e. the degree to which it resists to changes due to disturbance) and its resilience (i.e. the degree to which the initial community characteristics are restored after displacement). Habitat modification, as a consequence of disturbance, is an important factor in the invasion process. Disturbance in fact promotes invasion (Crawley, 1987; Hobbs, 1989; Mack and D'Antonio, 1998; Godfree *et al.*, 2004). For instance, the major disturbance on Banks Peninsula, as in other areas of New Zealand (McEwen, 1987; Rose *et al.*, 1998; Williams and West, 2000; Duncan *et al.*, 2001; McWethy *et al.*, 2009; Wilson and Meurk, 2011), can be found in the frequent fires with forest areas that were converted to grasslands for grazing by sheep and cattle, where there is a high intensity of oversowing of alien pasture species especially *Agrostis capillaris*, *Rytidosperma* spp., *Anthoxanthum odoratum*, *Lolium perenne* and *Poa pratensis*. As Parker *et al.* (2010) highlighted, areas converted from an agricultural to a forested state contain high numbers of alien species due to soil compaction. In reverted areas, the high levels of land-use activities (e.g. oversowing, fertiliser addition and livestock grazing) result in a high chance of dealing with high levels of invasion (Wilson and Meurk, 2011). Land managers will need to bear this in mind when considering future conservation or restoration programs on Banks Peninsula but also elsewhere.

6.4.2 Environmental drivers in heterogeneous landscape and applicability to other landscapes

The heterogeneous landscape and the natural history of the Banks Peninsula have presented me with a unique site for the study of plant invasions and for disentangling

the gradients of human-related disturbance and climate-topography. Many of the explanatory variables that have been used in my study are similar to previous studies where climate, environmental (e.g. topography) and potential human-related disturbance (e.g. land-use and propagule pressure) explained the distribution of alien species [e.g. Rouget and Richardson (2003); Pino *et al.* (2005)] and native species (Deutschewitz *et al.*, 2003; Dark, 2004) in less heterogeneous landscape (Boughton *et al.*, 2011) or at larger plot size (Marini *et al.*, 2009) or at smaller extent [e.g. < 12 km^2; Parker *et al.* (2010); Souza *et al.* (2011)]. Studies of native and alien plant species composition patterns in other modified landscapes have shown that the native and alien species communities differ in their spatial and ecological distributions together with the environmental factors with which they are correlated (Wilson *et al.*, 1989; Wilson, 1989; Oneal and Rotenberry, 2008; Brown and Boutin, 2009; Otýpková *et al.*, 2011). Two studies (Wilson, 1989; Wilson *et al.*, 1989) found that in other semi-natural to high managed pasture areas of the South Island in New Zealand, native and alien species communities differed spatially and ecologically and that these were differently related to environmental factors (e.g. elevation, soil fertility and water).

In brief and where the information is available, we need to take into account human-related factors or proxy measures (e.g. land-use change, fire frequency) and environmental gradients when studying drivers of plant invasions at local and regional landscape-scale, especially where the landscape is highly disturbed.

6.4.3 NARR scale dependence and factors related

Following my findings, the scale dependence of NARR is undeniable. Even when the plot size is small (< 100 m^2), as in the case of Banks Peninsula, and where the environments can be assumed to be relatively homogenous, habitat heterogeneity [i.e. diversity of habitats; *sensu* Franklin *et al.* (2002)] may still be encountered and it may still vary to the extent that NARR on Banks Peninsula (or studies worldwide that used the same plot size) significantly shifts from positive to negative and vice versa. Therefore, this high variability and the spatial dependence of NARR makes it difficult to disentangle the main drivers of NARR, not just on Banks Peninsula, but especially where the plot size used is large enough that the influence of other factors (e.g. climate and geology but also disturbance rates and propagule pressure) may be significant. This interplay of different factors that are involved, depending on which spatial grain/plot size is used, poses a considerable ecological challenge. Regarding

this, a question can be raised: is there an appropriate spatial grain/plot size to study an ecosystem for biological conservation purpose and ecological restoration? The scale dependence of ecological patterns and processes makes observations at one plot size often not applicable to other plot sizes (Wiens, 1989; Levin, 1992). In particular, findings from studies conducted at small spatial grain/plot size may not be extrapolated to large spatial grain/plot size (Rastetter *et al.*, 1992). As discussed in Chapter 3, Chapter 4 and Chapter 5, the NARR changes sign and magnitude according to different spatial grain/plot size and species communities. A negative NARR at small spatial grain/plot size and in native dominated communities is, in fact, opposed to a positive NARR at large spatial grain/plot size and in alien dominated communities. In the conservation biology context, this scale dependence poses a considerable challenge, given that there is a considerable number of detailed studies that involve small plot size (Gaston and Blackburn, 2000). Before embarking any decision, policy and decision makers need to bear in mind this scale dependence of NARR. Moreover, only few studies have included land-use and -management gradients (Peltzer and MacLeod, 2013). In my case study, I have shown that land-use and -management gradients are a significant factor in explaining NARR and therefore including a direct measure of human-related factors (e.g. land-use changes) may be important in arriving at a more precise measure of invasibility "to prioritize areas for invasive species control and prevention, for ecological restoration efforts that seek to create invasion resistant communities, and for understanding the processes that govern community assembly across a variety of ecosystems" (Fridley, 2011).

6.5 What is the broader ongoing research questions arising from the work?

Based on my work, I would like to recommend future study on a range of crucial issues in plant invasion ecology to provide a better basis for identifying new research ideas and avenues that will further build on the results of my study.

6.5.1 Sampling methods and GIS analysis for plant species and environment

In most cases, it is not possible to sample an area entirely. Therefore, in order to reduce some of the limitations in sampling species occurrence and environmental

data in the sampled area, it is desirable to formulate a priori hypotheses about which drivers may affect the species structure and patterns. If our study targets specific alien plant species and collects additional information regarding environments and conditions where these species are or are not located (Rew *et al.*, 2006; Hurst and Allen, 2007) this will also enable a fuller understanding of the processes and patterns of plant invasion. In addition, while several sampling methods may be used (e.g. grid and random points, random transects, roadside or adaptive survey sampling methods), we need to keep in mind which sampling methods best achieve the objectives/goals of our study (Maxwell *et al.*, 2012).

Different factors in the field can be measured to enhance the understanding of structure and patterns in species communities. In the context of Banks Peninsula, for example, a record of surrounding land-use types and grazing or burning history may have offered stronger explanatory power at the spatial grain and extent used. The NZLRI (NZLRI database; Landcare Research NZ Ltd., 2000) or LCDB (New Zealand Land Cover Database; Ministry for the Environment, 2013) or (EcoSat Woody; Landcare Research NZ Ltd., 2004) can also be used to quantify the proportion of woody vegetation within a circle of a given radius from the plot point. Otherwise, aerial photographs can be taken closer to the time of the floristic survey and the predictors recommended above derived by hand-digitising the extent of woody vegetation. These data would offer a stronger and independent assessment of land-cover, -use and -management. Once these data have been recorded and converted into GIS data layers of human-related disturbance along with soil processes (e.g. soil nutrient values) a fuller understanding of the drivers affecting native (and/or alien) plant species structure and patterns may be achieved. There is, in fact, a real need to combine GIS, Remote Sensing, spatial analysis and expert knowledge since further development of the interoperability of GIS and RS data and tools associated with spatial analysis would be a valuable technique in the study of native (and/or alien) plant species patterns at regional landscape and global scales.

6.5.2 NARR and biological homogenization: where do we go from here?

Ecologists have long been assessing community invasibility (Levine *et al.*, 2002) and while our understanding has advanced since Elton (1958), gaps still remain. If our desire for a general theoretical framework is to be realized, further investigation of NARR is required worldwide. My investigation into NARR has thrown up certain

contradictions which are difficult to explain. In my sutdy, the best moderator (i.e. plot size) explained "only" a maximum of 29% of NARR variability. Other factors, such as morphological or eco-physiological plant traits may be successfully related to native and alien species richness (Cantero *et al.*, 2003). Future studies of plant traits (e.g. growth rates, competitive abilities, dispersal modes) may explain a significant amount of variation in NARR (i.e. effect size) although there is an inherent difficulty in obtaining this information. Other possible significant drivers of NARR may also be found in the "Niche Differentiation Hypothesis (namely ND)" (MacArthur and Levins, 1967) and the "Habitat Filtering Hypothesis (namely HF)" (Keddy, 1992). ND at small spatial scale and HF at large spatial scale may explain greater variation of NARR, depending on the spatial scale of observation considered. Moreover, the paucity of studies that used unit of fixed grain on islands allows me to suggest that a future investigation of species richness on islands, using the quantitative approach I have developed here, may help us to resolve some of these contradictions and enable us to better understand NARR across habitats and ecosystems worldwide.

As stated, NARR is a measure to predict the vulnerability of ecological communities to invasion (Levine and D'Antonio, 1999; Lonsdale, 1999; Richardson and Pyšek, 2006) but it is also a measure to predict the likelihood of impacts on biodiversity, e.g. biotic homogenization (McKinney and Lockwood, 1999; Lambdon *et al.*, 2008; Winter *et al.*, 2009). Winter *et al.* (2009), for example, found that at regional scale, the combination of native plant extinctions (i.e. diminishing of native species richness) with plant invasions (i.e. increasing of alien species richness) decreased β-diversity among species communities leading to an homogenization effect of the European flora. Future work on biotic homogenization is undoubtedly needed. This will help us to determine general species patterns, for example, those across spatial grains and extent or elevational gradients and to better understand the roles of the related predictors. This will also help us to determine where biological homogenization is due to the cultivation of alien species or where it is a consequence of increasing invasion by alien species replacing native species (Spyreas *et al.*, 2004; Lambdon *et al.*, 2008; Hejda *et al.*, 2009). Furthermore, a systematic approach combining biological conservation and social concerns is required if we are to fully understand and moderate the consequences of such biological homogenization (Simberloff *et al.*, 2013).

Appendices

Appendix A

Datasheet for the Banks Peninsula floristic survey (1983-1998)

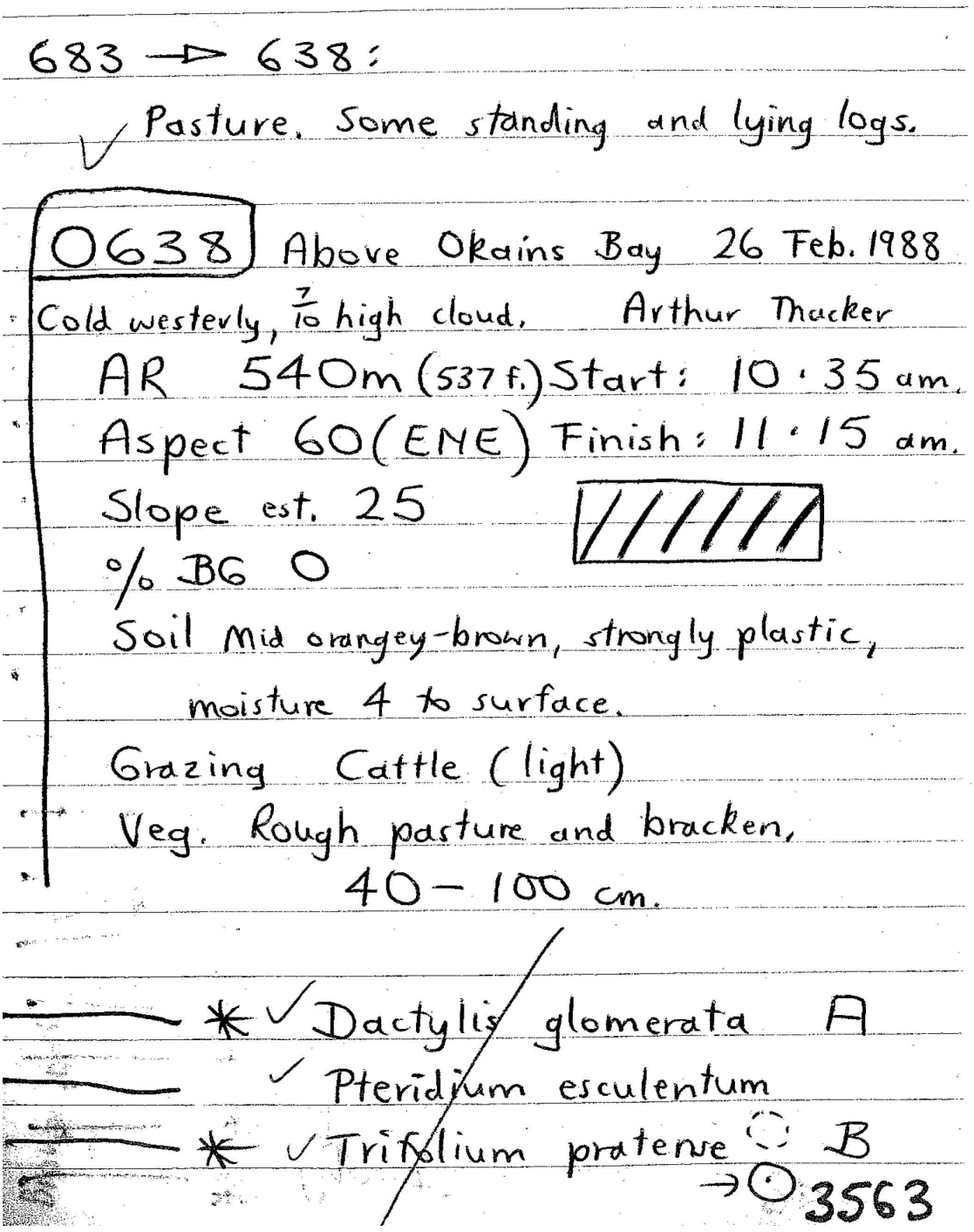

Figure A.1. Example of datasheets used in the Banks Peninsula floristic survey (1983-1998). From the top: the plot number, the environmental characteristics and the list of species in the plot.

Appendix B

GIS ModelBuilder application and layers from the Banks Peninsula geodatabase

To visualize the GIS model built in ArcGIS 9.3. for the Banks Peninsula geodatabase described in Chapter 2, use the following link:

http://mail.google.com

Username: f.tomasetto.phd.thesis

Password: f.tomasetto

Navigate to Drive

Select the folder Banks Peninsula geodatabase and the document
GIS ModelBuilder application

Plant species dataset and GIS layers are also contained in the Banks Peninsula geodatabse folder and they can be downloaded from GIS geodatabase species and layers files.

Appendix C

Visual Basic for Applications in ArcGIS 9.3 for distances

ArcGIS VBA Syntax:

Dim ET As New ETGW_Core

Set variable = ET.PointDistance (pInFeatureClass, pReferenceFeatureClass, sOutFileName, dSearchTol, pCalcSref)

The **PointDistance** method syntax has the following object qualifier and arguments:

Table C.1. Visual Basic for Applications (VBA) script that I used in in ArcGIS 9.3 model to calculate the distance for each plot of the floristic survey to the closest feature from another layer (Polyline or Polygon).

Part	Description
variable	An IFeatureClass object
pInFeatureClass	Required. An IFeatureClass object (Must be a point feature class)
pReferenceFeatureClass	Required. An IFeatureClass object (Polyline or Polygon feature class)
sOutFileName	Required. A String - the full name of the output feature class (A feature class with the same full name should not exist)
dSearchTol	Required. A Double representing the Search tolerance (in the units of the pCalcSref) to be used
pCalcSref	Required. A Spatial reference object which distance unit will be used for calculation

Appendix D

RMSE for the Digital Elevation Model downscaled

Table D.1. Summary results and RMSE for the Digital Elevation Model downscaled to a spatial resolution of 10 m (DEM 10). RMSE of the DEM of spatial resolution of 25m (DEM 25) are also presented.

	Min	**1st Quartile**	**Mean**	**Median**	**3rd Quartile**	**Max**	**SD**	**RMSE**
DEM 10	0	118.09	256.44	226	305.12	920	181.38	409
DEM 25	0	111.83	249.41	219	387.75	890	186.77	411

Appendix E

Multi-panel Cleveland dot plot for explanatory variables

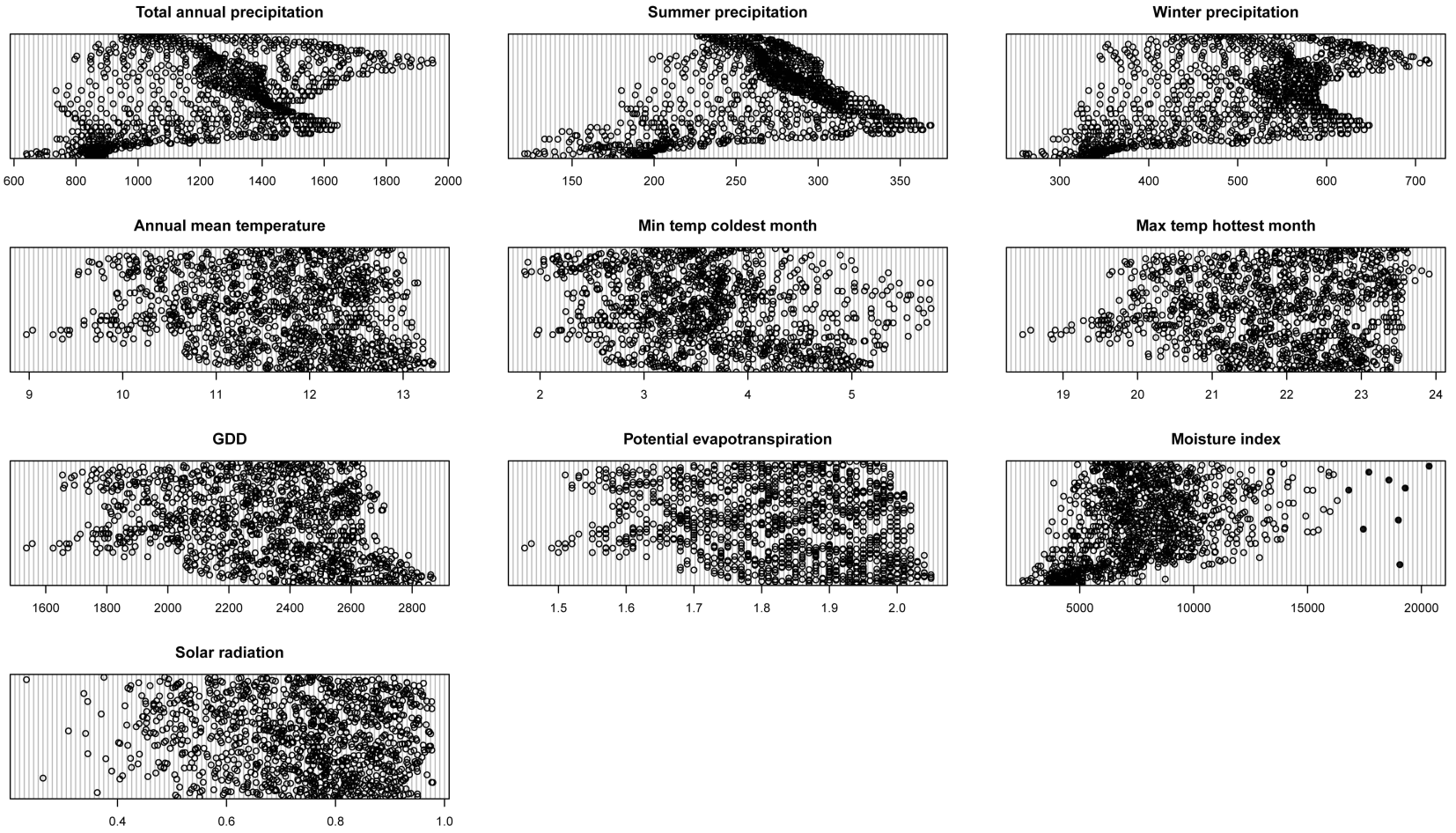

Figure E.1. Multi-panel Cleveland dot plot for climatic and bioclimatic variables. Values of a variable can be read from the x-axis, and by default the y-axis shows the order of observations in the variable (from bottom to top). Isolated points at the far ends, and on either side in a dot plot, suggest potential outliers. Outliers are shown as black fill dots.

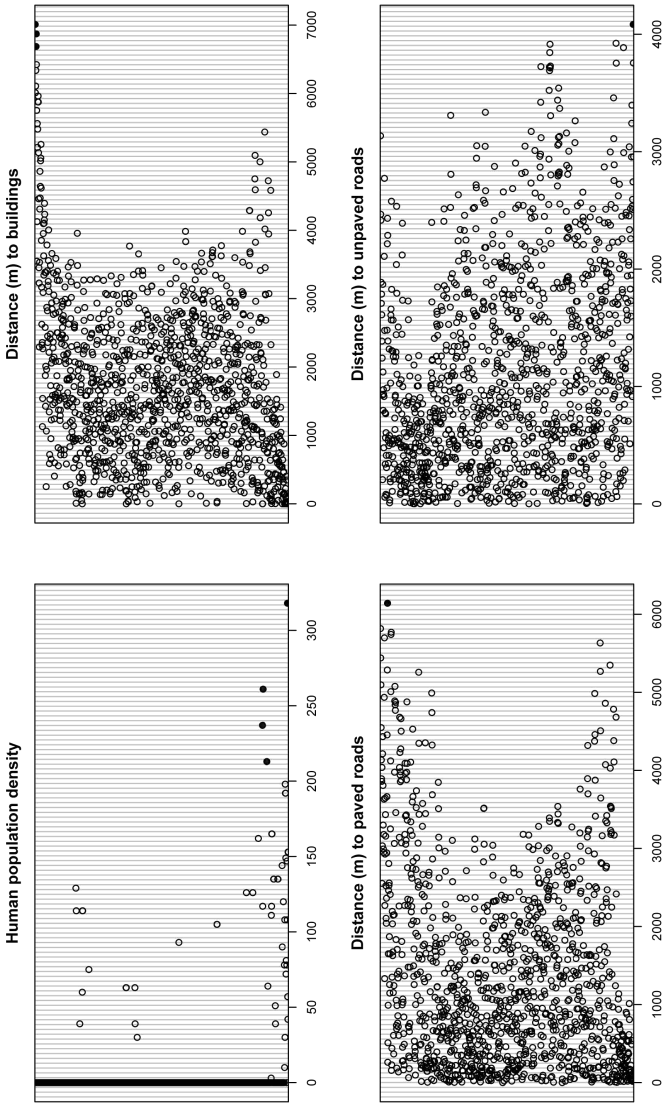

Figure E.2. Multi-panel Cleveland dot plot for the human-related variables. Outliers are shown as black fill dots.

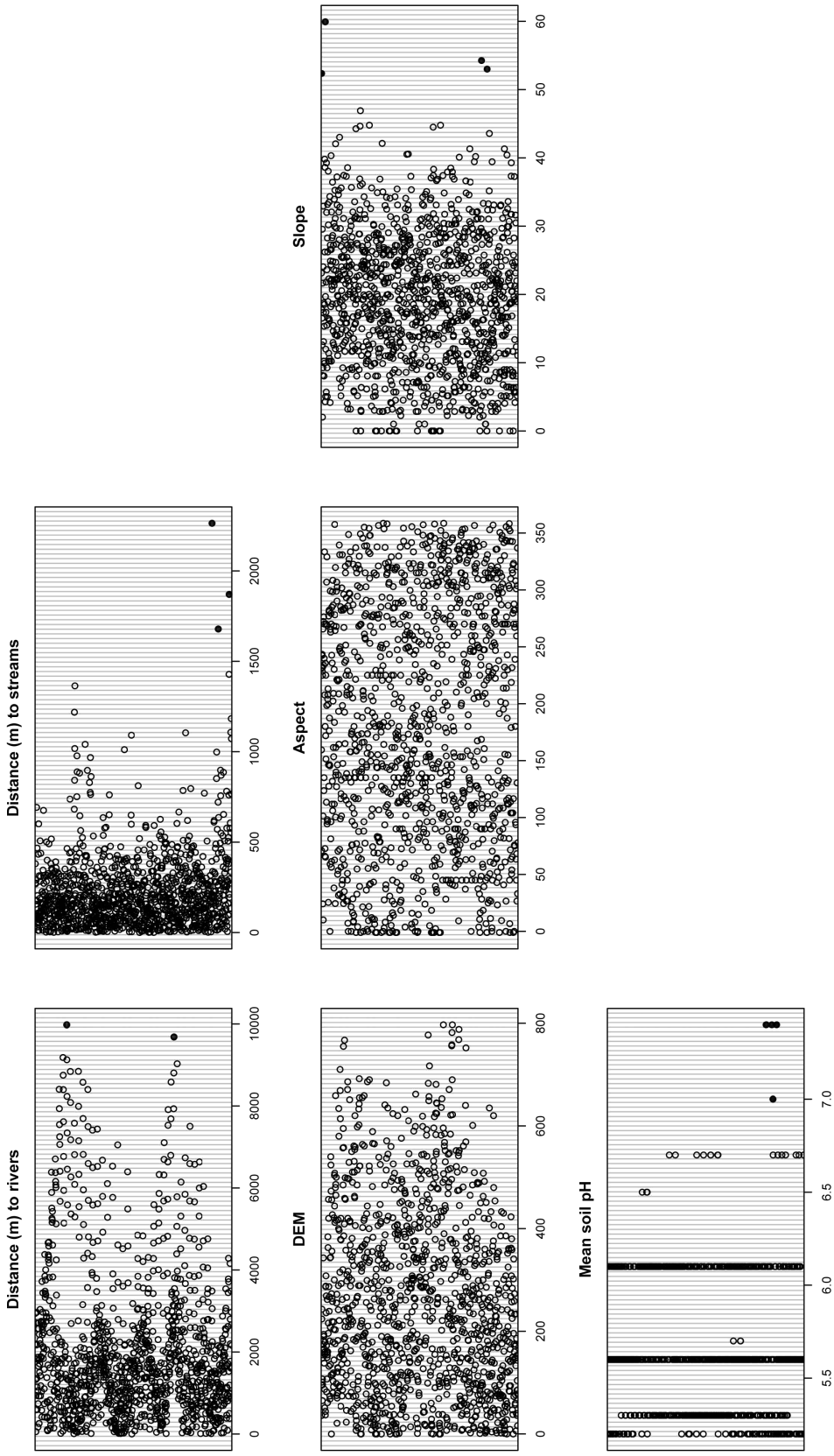

Figure E.3. Multi-panel Cleveland dot plot for the environmental variables. Outliers are shown as black fill dots.

Appendix F

Multi-panel scatterplots of continuous explanatory variables

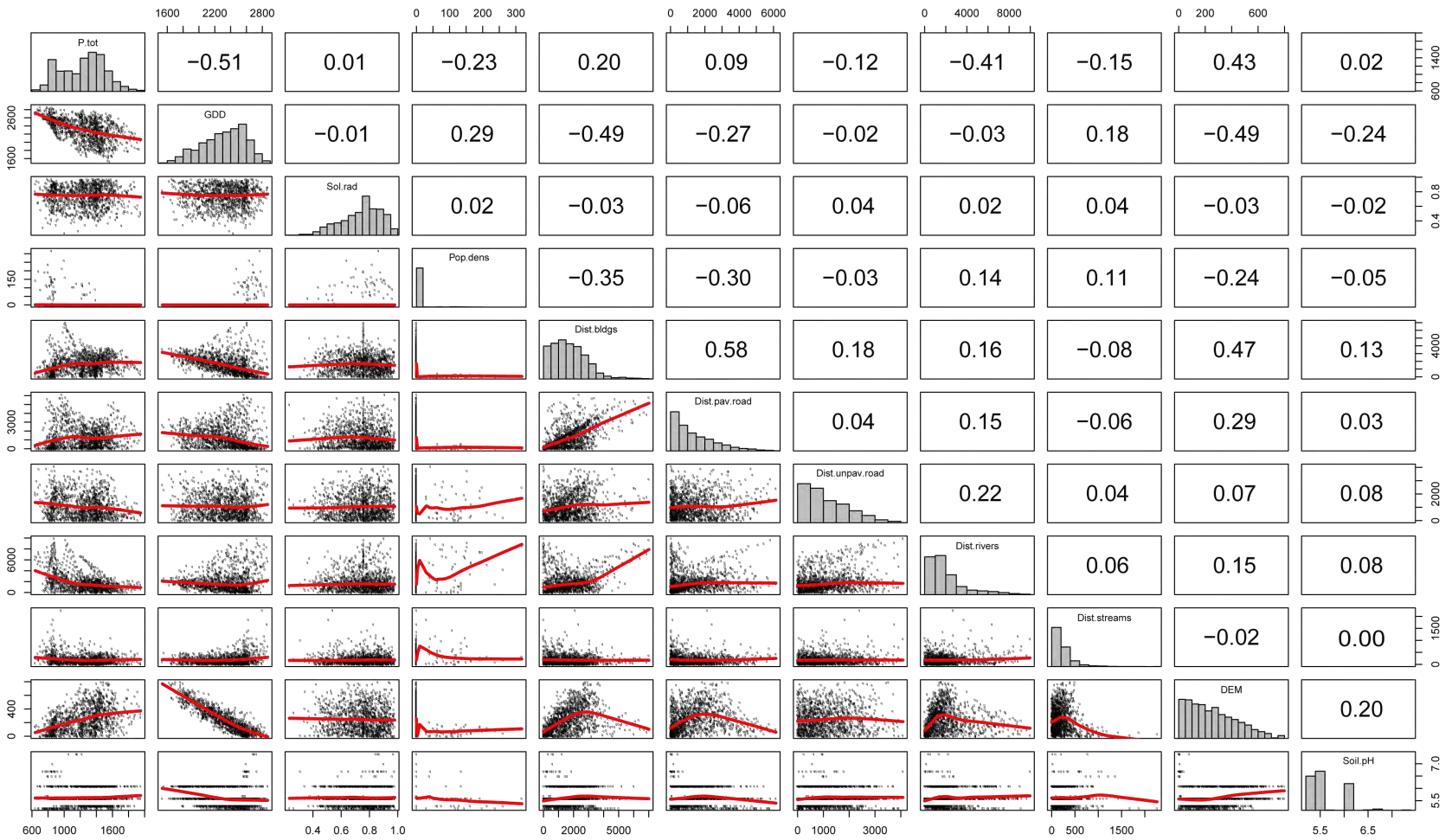

Figure F.1. Multi-panel scatterplots of 11 continuous explanatory variables. The upper panels contain estimated pairwise Spearman's rank correlations (*rho*). The diagonal panels contain histograms and the lower panels show pairwise scatterplots between each variable with a LOESS smoother (red line) added to aid visual interpretation. Further discussion of these variables will be found in Chapter 3 and Chapter 4.

Appendix G

Spatial autocorrelation coefficient (Moran's I) of explanatory variables

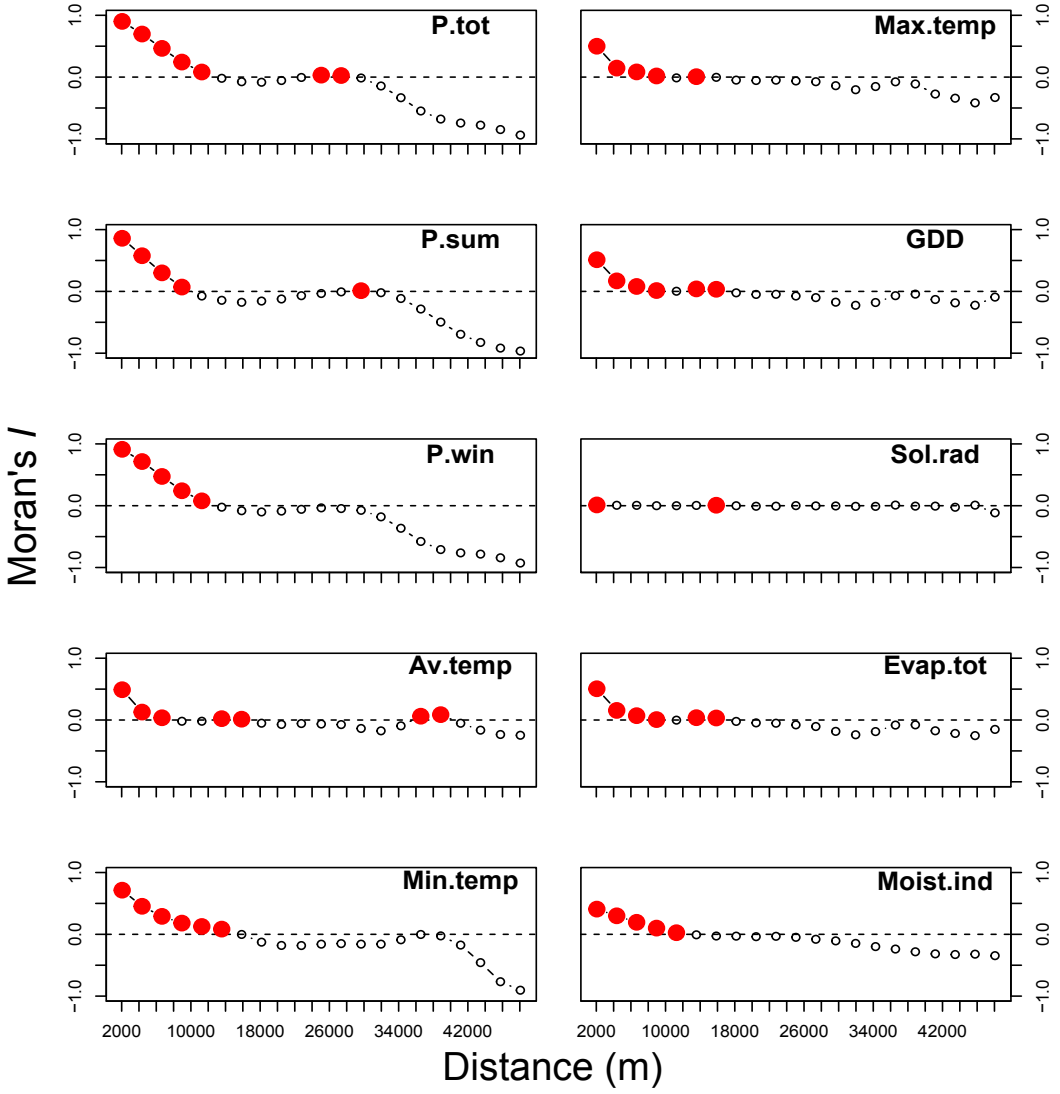

Figure G.1. Spatial autocorrelation coefficient (Moran's I) of climate variables calculated for 1227 points of the systematic sampling method. The red data points above the dotted horizontal lines in each panel indicate significant spatial autocorrelations based on randomization ($P < 0.001$), using the Monte Carlo randomized data ($n = 10000$ replicates).

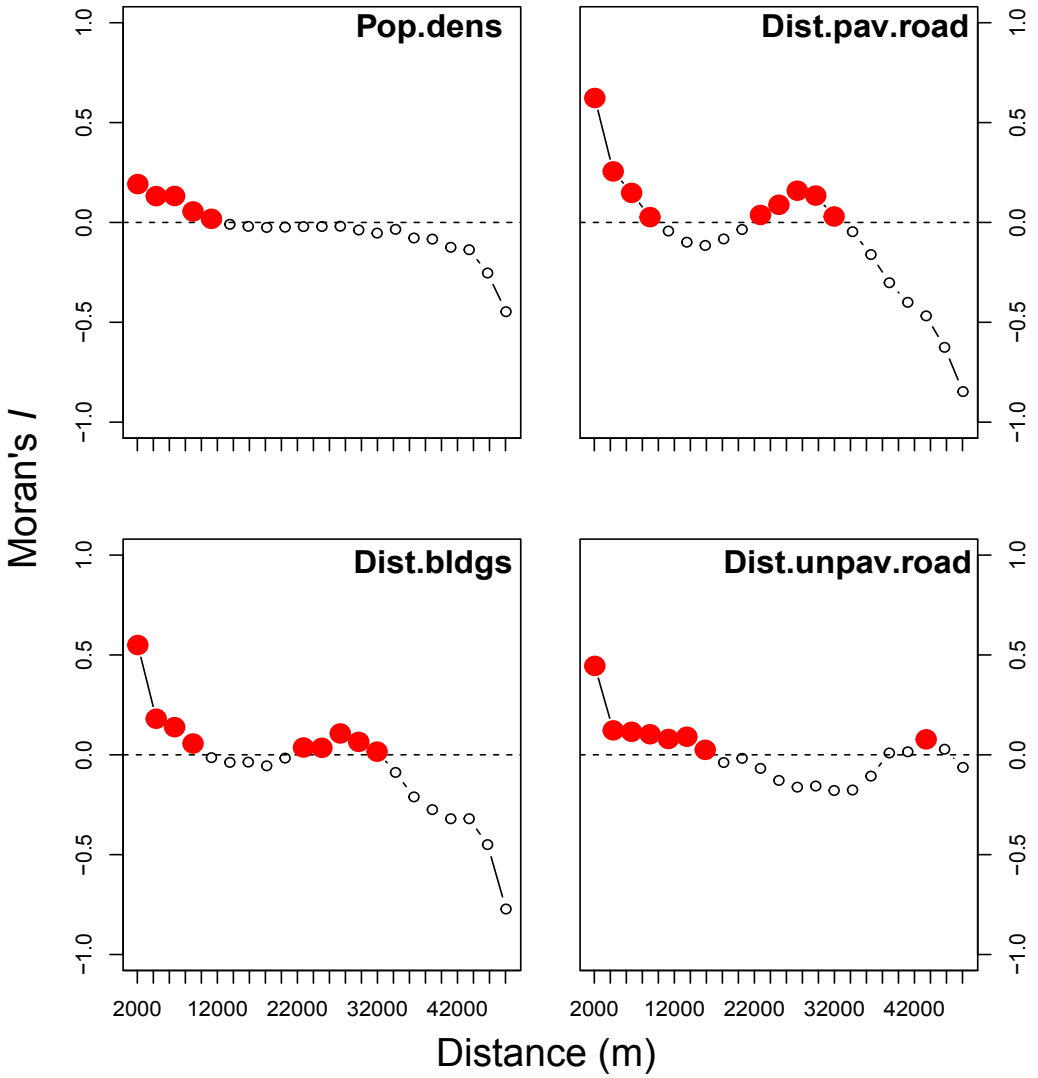

Figure G.2. Spatial autocorrelation coefficient (Moran's I) of human-related variables calculated for 1227 points of the systematic sampling method. The red data points above the dotted horizontal lines in each panel indicate significant spatial autocorrelations based on randomization ($P < 0.001$), using the Monte Carlo randomized data ($n = 10000$ replicates).

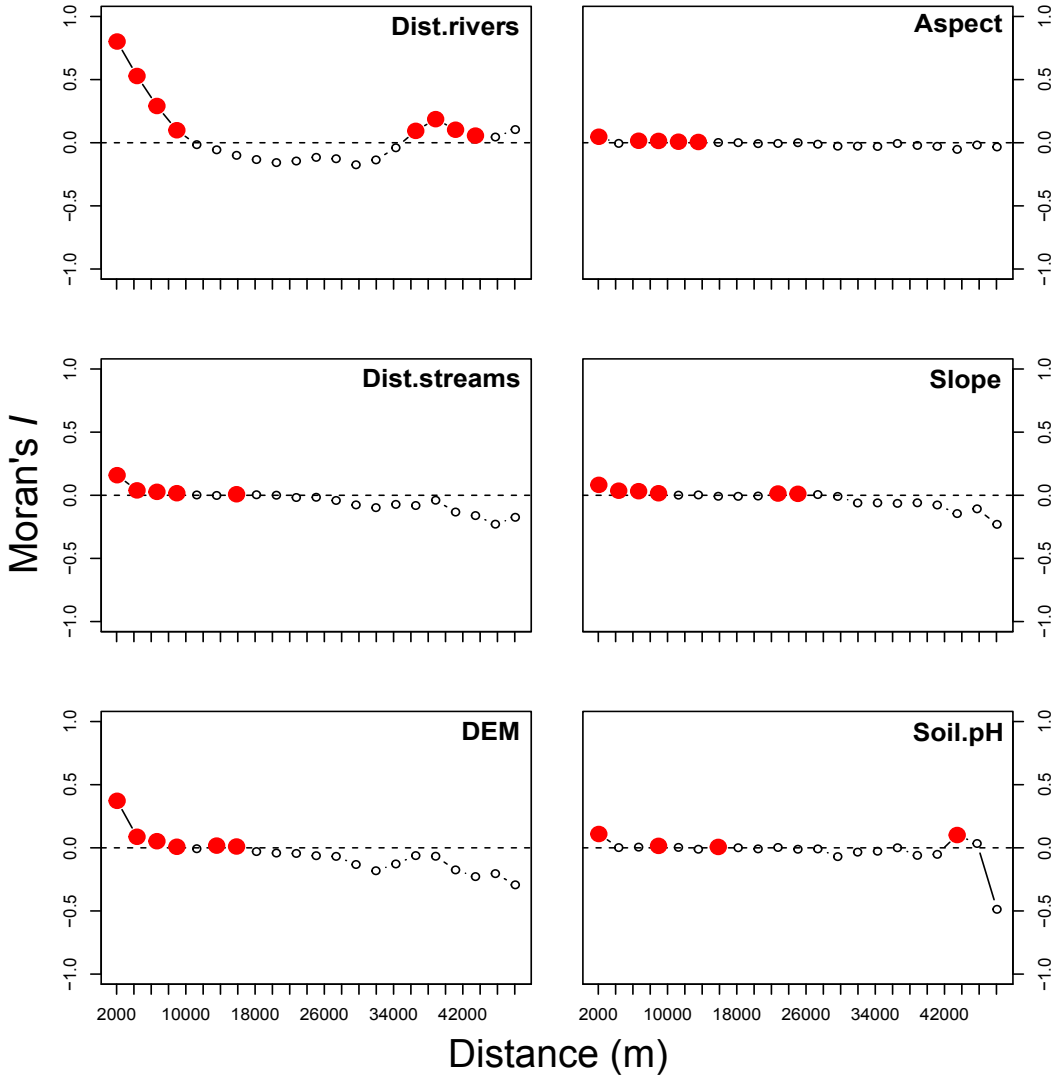

Figure G.3. Spatial autocorrelation coefficient (Moran's I) of environmental variables calculated for 1227 points of the systematic sampling method. The red data points above the dotted horizontal lines in each panel indicate significant spatial autocorrelations based on randomization ($P < 0.001$), using the Monte Carlo randomized data ($n = 10000$ replicates).

Appendix H

Full description of the eight community types identified by the clustering analysis

In the descriptions that follow I use the term native broadly to include species that are either endemic or indigenous to New Zealand (http://nzflora.landcareresearch.co.nz) or alien [i.e. casual or fully naturalized in the Canterbury region where Banks Peninsula is located; Wilson *et al.* (1992); Parsons *et al.* (1995); Mahon (2007); Wilson (2009)].

Type 1 is a highly-modified lowland ($\bar{x} = 134 \pm 12.3$ m) pasture community (111 alien grass species present) that were observed in 149 plots at more accessible plots and on less steep slopes ($\bar{x} = 12.4^{\circ} \pm 0.76$) with high GDD (*c.* 2453), relatively low annual precipitation of *c.* 1117 mm and close to buildings (*c.* 1162 m). The 93% of this community is dominated by fast growing alien species such as *Lolium perenne* (35 plots), *Dactylis glomerata* (22) and *Anthoxanthum odoratum* (19). The plots contain less native than alien species richness ($\bar{x}_n = 1.1 \pm 0.14$ and $\bar{x}_a = 17.2 \pm 0.45$, respectively) with ANR = 5.9 and a significantly positive species richness relationship ($rho = 0.33$, $P < 0.001$). Similarity index is 0.77 with a homogenization value of 0.14. The nestedness is high (3.17). Alien species occupy an order of magnitude greater than native species (8.23 ± 1.22 and 0.46 ± 0.07 separately).

Type 2 is a highly-modified rough pasture community (211 alien grass species present), that was observed in 266 plots at low- to mid-elevation ($\bar{x} = 263 \pm 9.6$ m) in less fertile soils with relatively high GDD (*c.* 2281), annual precipitation of *c.* 1165 mm and relatively close to buildings (*c.* 1322 m). To this community belong species such as *Agrostis capillaris* and *Cynosurus cristatus*. It is worth mentioning here that the use of fertilizers allows alien species such as *Lolium perenne*, *Anthoxanthum odoratum* and *Dactylis glomerata* to dominate 92% of the community plots. Alien species occupy an order of magnitude greater than native species (13.36 ± 2.53 and 1.62 ± 0.37 separately). Moreover, this community type showed the highest ANR (6.8) with a significant positive species richness relationship ($rho = 0.28$, $P < 0.001$). This community has the lowest value of similarity (0.65) but the highest values of homogenization (0.27) and nestedness (4.78).

Type 3 is mostly an alien pasture community with *Rytidosperma racemosum* (0.7) and *Trifolium glomeratum* (0.66) as indicator species. This grassland community tends to occur more in drier-poorer soil conditions, in area at low elevation ($\bar{x} = 156 \pm 10.1$ m) with *Silene gallica* (0.64) particularly along roads with the highest GDD (*c.* 2515), lowest annual precipitation of *c.* 992 mm and relatively close to buildings (*c.*

1550 m). Moreover, similarity index is 0.79 with homogenization index of 0.13 and the nestedness of this community is relatively high (2.56). Alien species occupy 8.58 $\pm$ 1.27 plots, while native species occupy 2.47 $\pm$ 0.55. ANR = 4.5 leads to a positive species richness relationship ($rho = 0.4$, $P < 0.001$), with 66% of this community dominated by alien grass such as *Lolium perenne* (22 plots), *Anthoxanthum odoratum* (16), *Cynosurus cristatus* (14).

Type 4 is mostly an alien grassland community (110 alien grass species present) with pasture species such as *Trifolium* spp. and *Rytidosperma clavatum* as most common indicator species. Moreover, 59% of this community is dominated by a pool of alien species such as *Lolium perenne*, *Anthoxanthum odoratum* with a relatively high values of homogenization (0.22) and nestedness of 2.05. Alien species occupy more plots than native ones (12.76 $\pm$ 2.1 and 3.29 $\pm$ 0.7 separately). This community is mostly related to warm and dry climatic conditions particularly at low- to mid-elevation plots ($\bar{x} = 208 \pm 8.4$ m) and on steep slopes ($\bar{x} = 20.1° \pm 0.6$) with relatively high GDD (*c.* 2411), low annual precipitation of *c.* 1164 mm and relatively close to buildings (*c.* 1717 m). The ANR of 4.5 leads to a positive species richness relationship ($rho = 0.35$, $P < 0.001$).

Type 5 is a mixture of native and alien grasses and shrubs with indicator species such as *Scandia geniculata* (0.39), *Galium aparine* (0.39) and *Coprosma virescens* (0.37) that were observed in 87 plots at low elevation ($\bar{x} = 160 \pm 16$ m), particularly in the coastal perimeter and cliffs of the Peninsula with the lowest GDD (*c.* 2053), relatively low annual precipitation of *c.* 1113 mm and relatively far from buildings (*c.* 1772 m). Alien species occupy slightly more plots than native species (3.54 $\pm$ 0.39 and 2.11 $\pm$ 0.24 separately). This vegetation type has the highest value of similarity (0.95) with low homogenization index (0.06). The nestedness is also relatively low (1.66). The ANR = 2.1 leads to a positive species richness relationship ($rho = 0.29$, $P < 0.01$). The 44% of this community is dominated by an alien species pool mainly composed of *Lolium perenne* (9 plots), but also with native grass (*Poa cita*, 7) and shrub (*Kunzea ericoides*, 7).

Type 6 is a semi-native tussock grassland community (32 native grass species present) with *Hydrocotyle novae-zeelandiae* var. *montana* (0.68), *Festuca novae-zelandiae* (0.64) and *Poa cita* (0.61) as indicator species. Within the elevational range in which this community type occurs ($\bar{x} = 302 \pm 17.2$ m), *Poa cita* can be

found more at the lowest elevations where *Festuca* spp. occurs at the highest elevation and on steep slopes with high annual precipitation of *c.* 1245 mm, low GDD (*c.* 2186) and far away from buildings (*c.* 2336 m). The plots show less native than alien species richness ($\bar{x}_n = 10.8 \pm 0.63$ and $\bar{x}_a = 15.3 \pm 0.27$, respectively) with ANR = 2.3. Homogenization is relatively high (0.23) and nestedness is 1.88. Alien species occupy relatively more plots than native ones (6.33 ± 1.27 and 3.79 ± 0.59 separately). Native grass *Poa cita* (22 plots) and alien grass such as *Lolium perenne* (12 plots) dominated 43% of the plots belonging to this community.

Type 7 is a semi-native tussock grassland community with indicator species such as *Pteridium esculentum* (indicator value 0.57), *Digitalis purpurea* (0.56), *Hydrocotyle moschata* (0.51) that was observed in 144 plots at mid- to high-elevation ($\bar{x} = 382 \pm 14.5$ m a.s.l.) and on steep slopes ($\bar{x} = 23.3° \pm 0.67$) with high annual precipitation of *c.* 1397 mm, relatively low GDD (*c.* 2103) and far from buildings (*c.* 1942 m). These plots contain high native and alien species richness ($\bar{x}_n = 13.9 \pm 0.64$ and $\bar{x}_a = 16.6 \pm 0.43$, respectively) with Alien Native richness Ratio (ANR) of 1.9 and nestedness (nest) of 1.8. Relatively high are similarity (0.79) and homogenization indices (0.12). Native species occupy less plots than alien ones (5.45 ± 0.58 and 7.67 ± 1.33 separately). The 66% of this community is dominated by native grass such as *Poa cita* (22 plots) and with 34% of this community dominated by a pool of alien grass species such as *Rytidosperma clavatum* (14), *Anthoxanthum odoratum* (12) and *Lolium perenne* (11).

Type 8 is the native second-growth forest and shrubland community which is widely spread in 111 plots at high elevation plots ($\bar{x} = 442 \pm 15.7$) and on steep slopes ($\bar{x} = 22° \pm 0.85$), particularly in gullies with GDD of *c.* 2185, high annual precipitation of *c.* 1365 mm and far from buildings (*c.* 2014 m). However, the nestedness is relatively low (2.25); 3% of this community is dominated by alien species. Native species occupy a greater number of plots than alien species (6.22 ± 0.69 and 1.41 ± 0.26 separately). Native shrub and tree species (36 and 28 species respectively) are the dominant species pool composed of *Poa cita* (25 plots), *Melicytus ramiflorus* (11), *Pteridium esculentum* (9) and *Fuchsia excorticata* (8). The plots contain less alien than native species richness ($\bar{x}_a = 3.9 \pm 0.43$ and $\bar{x}_n = 20.6 \pm 0.72$, respectively) with ANR = 0.2 leading to a significant negative species richness relationship (*rho* = -0.22, $P < 0.001$).

Appendix I

The elevational ranges and mean elevation of native and alien species

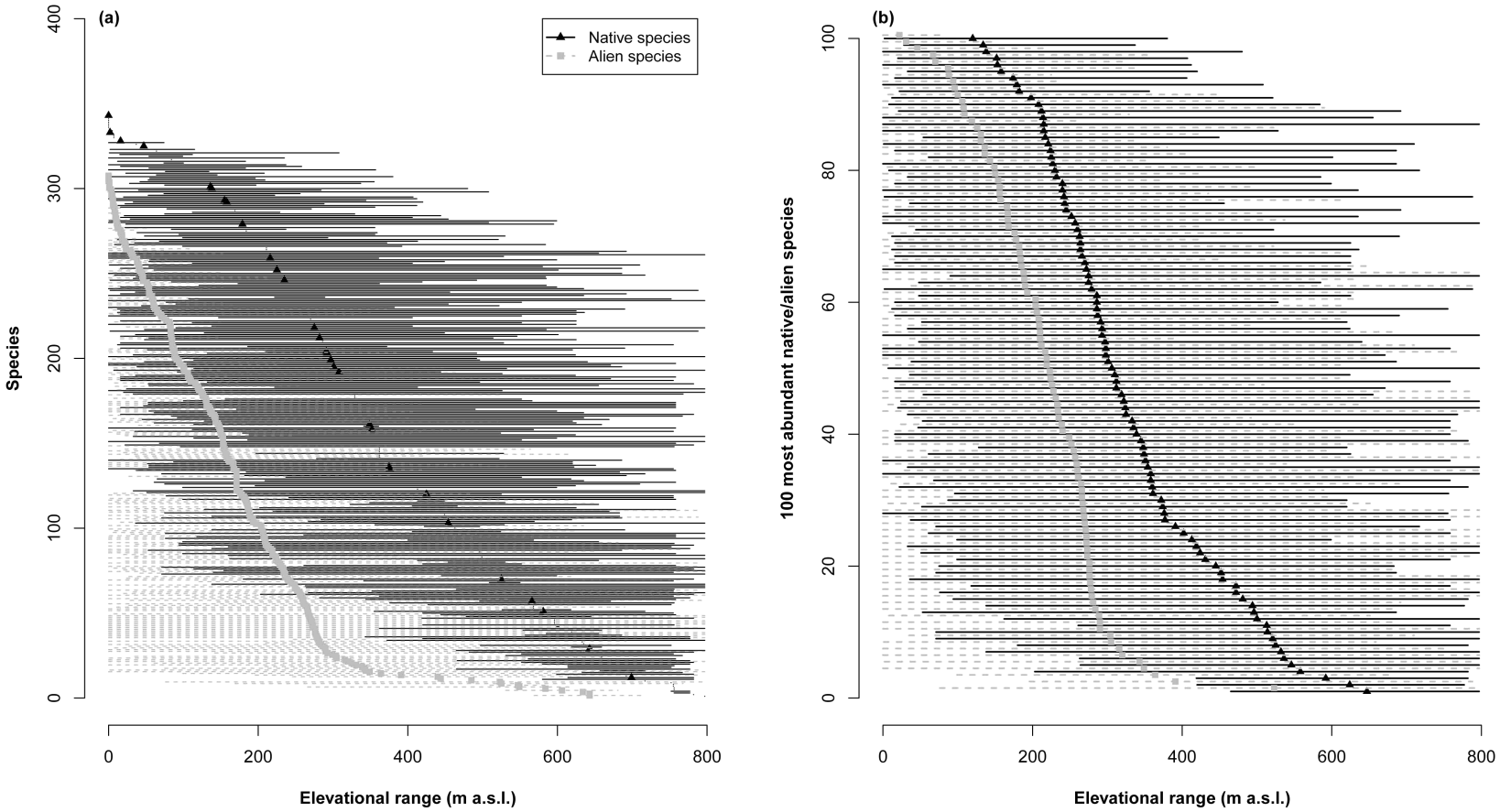

Figure I.1. The elevational ranges (black/grey dotted lines) and mean elevation of occurrence of the native (black triangles) and alien (grey squares) species recorded in each of the 1227 plots ordered by elevation of maximum occurrence. The graphs show: (a) the elevational ranges and mean elevation of 368 native and 311 alien species; (b) the elevational ranges and mean elevation of the 100 most abundant native and alien species.

Appendix J

Spatial patterns of eight community types

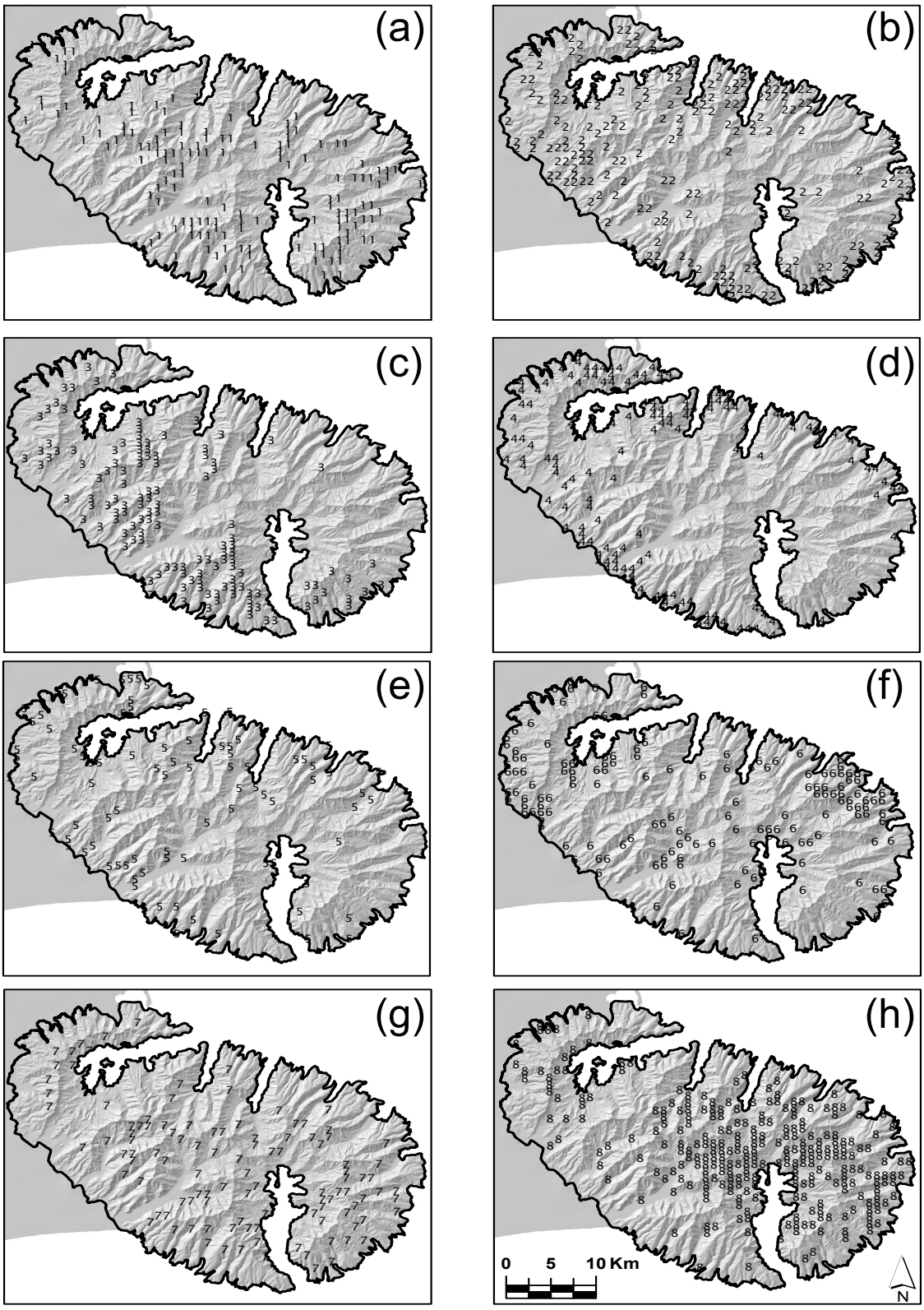

Figure J.1. Maps of Banks Peninsula (a-h) indicating approximately the positions of plots and plant community types according to the clustering analysis (see Chapter 3).

Appendix K

Native-alien plant species richness relationship paper

Diversity and Distributions, (Diversity Distrib.) (2013) **19**, 49–59

BIODIVERSITY RESEARCH

Environmental gradients shift the direction of the relationship between native and alien plant species richness

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ABSTRACT

Aim To assess how environmental, biotic and anthropogenic factors shape native–alien plant species richness relationships across a heterogeneous landscape.

Location Banks Peninsula, New Zealand.

Methods We integrated a comprehensive floristic survey of over 1200 systematically located 6 × 6 m plots, with corresponding climate, environmental and anthropogenic data. General linear models examined variation in native and alien plant species richness across the entire landscape, between native- and alien-dominated plots, and within separate elevational bands.

Results Across all plots, there was a significant negative correlation between native and alien species richness, but this relationship differed within subsets of the data: the correlation was positive in alien-dominated plots but negative in native-dominated plots. Within separate elevational bands, native and alien species richness were positively correlated at lower elevations, but negatively correlated at higher elevations. Alien species richness tended to be high across the elevation gradient but peaked in warmer, mid- to low-elevation sites, while native species richness increased linearly with elevation. The negative relationship between native and alien species richness in native-dominated communities reflected a land-use gradient with low native and high alien richness in more heavily modified native-dominated vegetation. In contrast, native and alien richness were positively correlated in very heavily modified alien-dominated plots, most likely due to covariation along a gradient of management intensity.

Main conclusions Both positive and negative native–alien richness relationships can occur across the same landscape, depending on the plant community and the underlying human and environmental gradients examined. Human habitat modification, which is often confounded with environmental variation, can result in high alien and low native species richness in areas still dominated by native species. In the most heavily human modified areas, dominated by alien species, both native and alien species may be responding to similar underlying gradients.

Keywords

Biological invasions, biotic interactions, climate, exotic species, land-use change, scale dependence, weeds.

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INTRODUCTION

Understanding the factors that underpin the relationship between native and alien plant species richness is of central importance in invasion biology because it provides a means to predict the vulnerability of ecological communities to invasion (Levine & D'Antonio, 1999; Lonsdale, 1999; Richardson & Pyšek, 2006) and the likelihood of impacts on

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biodiversity, for example biotic homogenization (Lambdon *et al.*, 2008; Winter *et al.*, 2009). There is an emerging consensus that the relationship between native and alien plant richness is scale dependent, often being negative when assessed across small spatial grains and extents but positive as the scales of observation increase (Fridley *et al.*, 2004, 2007; Hulme, 2008). The explanation for this changing relationship, termed the 'invasion paradox' (Fridley *et al.*, 2007), is framed in the context of a resident native community being invaded by alien species. For small spatial grains (e.g. plots < 100 m^2) and small extents (e.g. < 10 km^2), where the environment can be regarded as relatively homogenous and biotic interactions are likely to influence species co-occurrence, sites with more resident native species are better able to resist invasion by aliens through competitive exclusion, leading to a negative relationship between species richness (Levine & D'Antonio, 1999; Herben *et al.*, 2004). For larger spatial grains (e.g. plots $\geq$ 100 m^2) and larger extents (e.g. $\geq$ 10 km^2), encompassing greater spatial heterogeneity, variation among plots in native species richness primarily reflects the variation in underlying environmental conditions, including changes in resource availability, levels of disturbance or proximity to propagule sources (Stohlgren *et al.*, 2006; Fridley *et al.*, 2007; Hulme, 2008). Alien species should respond to these large-scale gradients in a similar manner to native species such that sites where conditions favour high (or low) native richness should likewise favour high (or low) alien richness, leading to a positive relationship between the two.

The evidence to date supports the expectation that native–alien richness relationships are positive at large plot sizes, which is usually interpreted as the result of both native and alien plant species responding to similar gradients in resource availability and habitat heterogeneity at a broad scale (Stohlgren *et al.*, 2006). However, studies that use small plots, while more suited to identifying patterns associated with biotic interactions between native and alien plant species, typically show more variable outcomes with both positive and negative relationships common (Stohlgren *et al.*, 1999, 2006). This variability has been interpreted as a statistical problem associated with very small plots (1–10 m^2) that fail to adequately sample the plant community resulting in high variance in native and alien plant richness because of high spatial turnover in species composition (Stohlgren *et al.*, 1999). Nevertheless, variability in the native–alien richness relationship might also arise for ecological reasons. A wealth of studies have highlighted that native and alien species can differ in their distribution, particularly in relation to anthropogenic impacts that can alter the representation of species through changes in the regional species pool via increased propagule pressure of aliens (McKinney, 2002; Arévalo *et al.*, 2005; Lockwood *et al.*, 2005; Aikio *et al.*, 2012), alterations in the disturbance regime through fire and grazing (Hobbs & Huenneke, 1992; D'Antonio, 2000; Keeley *et al.*, 2003), changes in soil nutrient status as a consequence of atmospheric or agricultural fertilization (Dukes & Mooney, 1999), other forms of land management (e.g. highly managed or semi-natural pastures; Boughton *et al.*, 2011) or land-use history (e.g. ongoing reforestation; Parker *et al.*, 2010). Considerable effort has been invested in disentangling the role of environmental factors from anthropogenic factors in determining the richness of native and alien plants (Gilbert & Lechowicz, 2005; Carboni *et al.*, 2010; Bartomeus *et al.*, 2011), given that human pressure is generally correlated with better climate (Hanspach *et al.*, 2008; Marini *et al.*, 2009, 2012). While native and alien species richness can be positively associated with some anthropogenic gradients (e.g. human population density; Marini *et al.*, 2009), they can be negatively or not associated with others (e.g. land management intensity; Boughton *et al.*, 2011). Consequently, positive and/or negative relationships between native and alien plant richness may be found within the same landscape depending on the character, magnitude and variation in the dominant environmental or anthropogenic gradients.

In this study, we explore the relationship between native and alien plant species richness in over 1200 vegetation plots (36 m^2) systematically distributed across a heterogeneous landscape (*c.* 1000 km^2) on Banks Peninsula, New Zealand. The Banks Peninsula has a variable topography (0–920 m a.s.l.) associated with strong gradients in climate, land-use history and management, and distribution of human population. We used these data to address the following questions:

1. What is the overall relationship between native and alien plant species richness and how strongly is it shaped by variation in anthropogenic and environmental gradients?

2. Do similar native and alien relationships hold in plant communities that have either experienced relatively high or low human impact and are respectively dominated by either alien or native species?

3. What is the relative contribution of environmental and anthropogenic gradients to the relationship between native and alien plant species richness?

METHODS

Study area

Banks Peninsula (*c.* 1000 km^2) in the south-east coast of the South Island, New Zealand (43°33′–43°54′S, 172°37′–173°7′E), comprises the eroded remnants of two large shield volcanoes, creating a highly varied topography that ranges in altitude from 0 to 920 m above sea level (see Fig. S1 in Supporting information). Soils are derived from basaltic volcanic rock and loess (Sewell *et al.*, 1992) and are typically well drained and of moderate to high fertility (Speight, 1943; Williams, 1983; Sewell *et al.*, 1992; Wilson, 2009). Annual rainfall ranges from 600 mm at the driest low-elevation sites to 2000 mm at higher elevations, and mean daily temperature ranges from 8 to 13°C. Banks Peninsula was almost entirely forested prior to human colonization of New Zealand, but following European settlement in the mid-1800s forest was extensively cleared and converted to grassland for farming,

such that by 1920, < 1% of the original forest cover remained (Wilson, 2008, 2009). In less intensively farmed areas, typically at higher elevation and in less-accessible locations, forest clearance and burning has led to forest replacement by grassland dominated by native tussocks, particularly native *Festuca* spp., *Poa* spp. and *Chionochloa* spp. These tussock grasslands are typically associated with an intertussock sward comprising a mixture of native and alien grasses and herbs. On more accessible and productive, typically low- to mid-elevation sites, more intensive burning, oversowing with pasture species, fertilizer addition and livestock grazing led to the removal of native tussocks and their replacement by grasslands dominated almost entirely by improved alien pasture species. During the last several decades, some areas of less intensively managed farmland have been abandoned and left to regenerate back to native shrubland and forest. The present landscape thus comprises a mosaic of about 10% original or regenerated native forest, 5% native shrubland (< 6 m tall) and 85% grassland ranging from less-modified areas of semi-native tussock grassland to highly modified pastures dominated by alien grasses such as *Lolium perenne*, *Dactylis glomerata* and *Cynosurus cristatus* (Wilson, 1994, 1999). This gradient in vegetation, from native forest to shrubland to semi-native tussock grassland to alien-dominated pasture, covaries with elevation but principally reflects a gradient in anthropogenic impacts, moving from sites less modified by burning, grazing, fertilizer addition and oversowing of improved alien pasture species to sites that have been heavily modified by these processes. Human population density is low in the region, with approximately 7000 people living on the Peninsula and largely concentrated in three major settlements: Akaroa, Diamond Harbour and Little River (Statistics New Zealand, 2006).

Floristic data

We used data from a comprehensive floristic survey conducted between 1983 and 1988 that comprised a total of 1260 plots systematically located at each intersection of a regular 1000 × 1000 yard grid (*c.* 920 × 920 m) drawn over the entire Banks Peninsula (Wilson, 1992). A 6 × 6 m plot, a common scale for vegetation sampling (Mueller-Dombois & Ellenberg, 1974), was located at the intersection of each grid, within which the species composition of all vascular and non-vascular plant species was recorded and each species was ranked according to its relative abundance in the plot. The plot aspect and slope were also recorded. The 36-m^2 plot size is consistent with recommendations for adequately sampling grassland vegetation in New Zealand (Hurst & Allen, 2007) and Europe (Chytrý & Otýpková, 2003; Otypková & Chytry, 2006). Furthermore, given that there is no agreed optimum plot size at which to assess the relationship between native and alien species richness, a plot size of 36 m^2 appears a reasonable compromise, being large enough to adequately sample the community while not being so large as to mask patterns arising from biotic interactions.

In our analyses, we considered only vascular plant species and excluded 33 plots without any vascular species, leaving a total of 1227 plots. Plant species were classified as native or alien to New Zealand following the standard definitions (New Zealand Plant Names database – available at http://nzflora.landcareresearch.co.nz; Parsons *et al.*, 1995; Mahon, 2007), and we calculated the total number of native and alien species per plot, which we used as our response variables. We classified each plot as either 'alien dominated' or 'native dominated' based on whether the species ranked as the most abundant in each plot was an alien or a native species, respectively. We further classified each species as a tree (woody species ≥ 6 m tall), shrub (woody species < 6 m tall including lianes), fern, herb or grass using the trait categories in Ecological Traits of New Zealand Flora (available at http://ecotraits.landcareresearch.co.nz/) and calculated the relative proportions of these groups in each plot. Species nomenclature follows *Flora of New Zealand* (Moore & Edgar, 1970; Healy & Edgar, 1980; Allan, 1982; Webb *et al.*, 1988; Edgar & Connor, 2000).

Explanatory variables

For each plot location, we estimated the values of climate, environmental and human-related variables from spatially explicit data layers in a GIS database (Table S1) that might explain variation in species richness. We initially identified nine climate variables known to influence the growth and distribution of plants but problems of colinearity (e.g. $r > 0.5$) resulted in selecting only three: annual precipitation, growing degree days and potential solar radiation as key climate variables that captured the major precipitation and temperature gradients. Climate variables were obtained from the National Institute of Water and Atmospheric Research (NIWA) 500 × 500 m resolution climate maps (Tait, 2007; Tait & Zheng, 2007). Potential solar radiation (a measure of the amount of radiation per unit area reaching the earth's surface as a proportion of the amount received at the equator) was calculated from latitude, aspect and slope of each plot (Kaufmann & Weatherred, 1982). We selected four other environmental variables: elevation, distance to the nearest river and stream, and mean soil pH. Elevation data were obtained from a Digital Elevation Model (DEM) downscaled to a resolution of 10 m but was not used in some analyses because of its high colinearity with climate variables (e.g. $r \geq 0.5$). Riparian areas are known to be vulnerable to invasion by alien species, especially when subjected to human-induced disturbances (Aguiar *et al.*, 2001; Parks *et al.*, 2005; Maskell *et al.*, 2006). We therefore included the distance of each plot to the nearest permanent river (a large natural permanent flowing water body) or stream (a perennial or intermittent tributary of a permanent river), as defined in the New Zealand River Environment Classification (REC; Ministry for the Environment, 2010). An estimate of mean soil pH at each plot (0.2–0.6 m depth) was obtained from polygon layers derived from stereo photograph

interpretation, field verification and measurement as part of the 1:63.000/1:50.000 scale New Zealand Land Resource Inventory survey (NZLRI database; Landcare Research, 2000) integrated with the National Soils Database (NSD; Wilde, 2003).

As human habitation and roads may be important sources and conduits of alien plant dispersal (Timmins & Williams, 1991; Hobbs, 2000; Sullivan *et al.*, 2005; McKinney, 2006), we included four human-related variables: distance to nearest built-up area, local population density, and distance to the nearest paved or unpaved road. We calculated the distance (m) of each plot centre to the nearest built-up area (or buildings) and estimated the human population density proximate to each plot using the *1991 New Zealand Census* book (Statistics New Zealand, 1991). We georeferenced and photointerpreted nine orthorectified aerial photographs from the early 1990s (2.5 × 2.5 m spatial resolution) of Banks Peninsula derived from Land Information New Zealand (LINZ – available at http://www.linz.govt.nz/) to identify built-up areas. Those areas were classified as areas with at least three houses or other buildings in an area of at least 1.012 ha (U.S. Geological Survey Land Cover Institute definition). To ensure accuracy of the locations of settlements from aerial photographs (such as built-up areas or buildings), particularly those close to vegetation plots, we undertook field verification. To determine whether land-use history and management of the Peninsula shape the relationship between native and alien species richness, we also included the relative proportion of native trees in each plot which reflects a gradient in anthropogenic impact from less-modified areas of native forest and shrubland with a high native woody component to more heavily modified grasslands. To quantify how additional biotic factors shape the relationship between native and alien plant species richness, we also included separately native richness and alien richness as explanatory variables.

Statistical analysis

All spatial data were stored and extracted using ArcGIS 9.3 (Esri, 2009), and all statistical analyses were performed in R (2.13.0; R Development Core Team, 2011). We first quantified the relationship between native and alien richness across all plots using Spearman's rank correlation, because this measure is less sensitive and more robust than Pearson's correlation to outliers. Once we had verified that any outliers were not sampling errors, we then examined the relationship between native and alien richness separately for plots where the dominant plant species was either an alien or a native. We also assessed the correlations between native and alien species richness and the proportions of trees, shrubs, herbs and grasses because variation in the representation of these life forms reflect a gradient in intensity of past land use.

We then fitted a multiple regression model to identify factors that could explain the variation in native and alien species richness. To account for spatial autocorrelation, we fitted the regression models with a spatial autocorrelation structure using generalized least squares (GLS; Legendre, 1993; Dormann, 2007). We assessed the potential influence of spatial autocorrelation on parameter estimates by modelling different spatial correlation structures (Pinheiro & Bates, 2009) and using the Akaike Information Criterion (AIC; Akaike, 1974; Burnham & Anderson, 2002; Johnson & Omland, 2004) to identify the best model (Pinheiro *et al.*, 2011). We assessed the degree to which our models accounted for unexplained spatial variation by plotting a semi-variogram of the normalized residuals.

We also examined whether explanatory variables showed a nonlinear relationship to the response by testing for the importance of quadratic terms. Only soil pH showed a strong nonlinear relationship with species richness, so we included this variable along with its quadratic term in the multiple regression model.

Given the large elevation range on Banks Peninsula and the covariance of anthropogenic impacts with elevation, we also examined how the native–alien species richness relationship varied across this gradient by examining the correlation between native and alien species richness separately for plots in five elevational bands (0–100, 101–200, 201–300, 301–400 and > 400 m a.s.l.) chosen to ensure that each band had an approximately equal number of plots. Stratifying plots by elevational bands ensures key climate variables (such as temperature and precipitation) remain within a narrow range and allows us to examine the relationship between native and alien richness having controlled for this variation (Hanspach *et al.*, 2008; Marini *et al.*, 2009, 2012).

RESULTS

Relationships between native and alien species richness

Although slightly more native (368) than alien (311) vascular plant species were recorded in the 1227 plots on Banks Peninsula, on average over twice as many alien (16.4 ± 0.19) as native species (7.9 ± 0.23) were found per plot (Wilcoxon rank sum test: $W = 120$, $P < 0.001$). Across all plots, native and alien plant species richness were significantly negatively correlated (Spearman's rank correlation, $\rho = -0.126$, d.f. = 1227, $P < 0.001$; Fig. 1a). However, fitting a cubic smoothing spline to the data suggested that the relationship was nonlinear. For plots with fewer than about 10 native species, the relationship between native and alien richness appeared positive, while for plots with more than 10 native species, the relationship was strongly negative. Over 60% ($n = 739$) of plots were classified as alien dominated, with the majority being grassland plots dominated by introduced pasture species such as *Lolium perenne* (dominant in 189 plots), *Cynosurus cristatus* (89 plots) or *Dactylis glomerata* (83 plots). Alien-dominated plots typically had low native species richness and comprised the majority of plots with fewer than

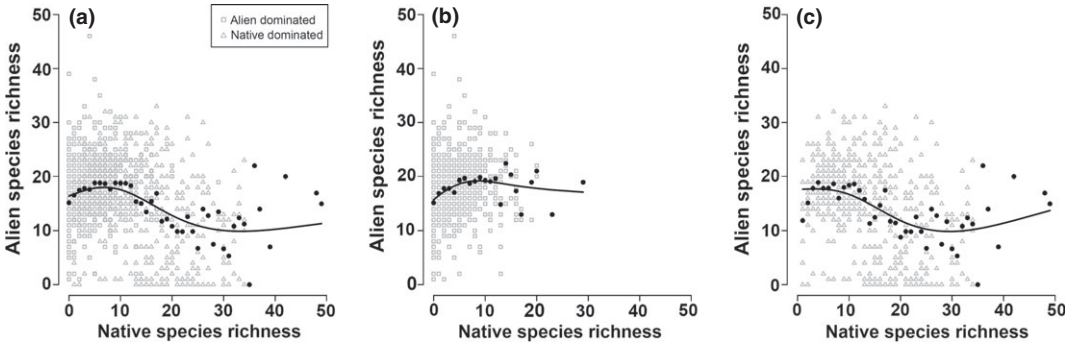

Figure 1 Relationship between native and alien plant species richness across the Banks Peninsula, New Zealand in: (a) all 1227 plots ($\rho = -0.126$, $P < 0.001$); (b) alien-dominated plots (739 plots, $\rho = 0.26$, $P < 0.001$); (c) native-dominated plots (488 plots, $\rho = -0.34$, $P < 0.001$). Grey points are individual plots; black points show the mean value of alien species richness for each value of native species richness. Solid lines show a cubic smoothing spline fitted to the full data set.

10 native species. The 488 plots dominated by a native species included modified tussock grassland dominated by *Poa cita* (94 plots) and *Rytidosperma clavatum* (52 plots), along with native forest and shrubland communities dominated, for example, by *Kunzea ericoides* (53 plots). Native-dominated plots included the majority of plots with more than 10 native species. The separation of plots into those dominated by alien or native species largely accounted for the nonlinear relationship between native and alien species richness seen across all plots (Fig. 1a). For alien-dominated plots, with low native but high alien species richness per plot (3.9 ± 0.15 and 17.5 ± 0.19, respectively), there was a significant positive relationship between native and alien richness ($\rho = 0.26$, $P < 0.001$; Fig. 1b). In contrast, the species richness relationship was stronger and significantly negative in native-dominated plots ($\rho = -0.34$, $P < 0.001$; Fig. 1c) with similar mean values of alien and native richness per plot (14.7 ± 0.36 and 14.1 ± 0.4, respectively).

Across all plots, the dominant species life forms shift along the gradient of increasing native species richness. Plots with low native species richness have a higher proportion of alien grass and herbaceous species ($\rho = -0.59$ and $\rho = -0.27$, $P < 0.001$ respectively), while plots with high native species richness contain a higher proportion of native trees and shrubs ($\rho = 0.59$ and $\rho = 0.7$, $P < 0.001$, respectively, Table 1). These patterns remain when native- and alien-dominated plots are examined separately. Native-dominated plots with low native species richness have a higher proportion of grass and herbaceous species ($\rho = -0.69$ and $\rho = -0.39$, $P < 0.001$, respectively), while those with high native species richness contain a higher proportion of tree and shrub species ($\rho = 0.62$ and $\rho = 0.69$, $P < 0.001$, respectively). For alien-dominated plots, the same gradient is apparent where plots with high native species richness have a higher proportion of native tree and shrub species ($\rho = 0.29$ and $\rho = 0.51$, $P < 0.001$, respectively), while plots with high alien species richness have more grass and herbaceous species ($\rho = 0.32$ and $\rho = 0.37$, $P < 0.001$, respectively).

Determinants of native and alien richness

Low but significant spatial autocorrelation was consistently found in the residuals of our GLS, and thus, we report results based on these spatial models. Plots with high native richness (containing a higher proportion of tree and shrub species) were more likely to occur at cooler sites (typically at higher elevation) with low solar radiation (steeper, south-facing slopes), intermediate in soil pH, in areas with lower alien richness that were further away from unpaved roads (Table 1). In contrast, plots with higher alien species richness (dominated by grass and herbaceous species) occurred on warmer sites (typically at lower elevation) with high solar radiation (drier north-facing slopes) that had low native species richness and intermediate soil pH (Table 1). Hence, at a broad scale, plots with high native and alien species richness were spatially separated and tended to occupy different parts of the landscape. However, these edaphic factors only accounted for 21% and 9% of the variation in native and alien species richness, respectively. Alien richness in the native richness model and vice versa explained a small but significant amount of additional variation (increasing the variation accounted for to 23% and 11%, respectively; Table 1), indicating that unmeasured factors linked with biotic suitability further shaped species richness patterns.

These relationships were also evident within alien- and native-dominated plots (Table 1). Within each of these groups, alien richness tended to be higher on warmer (lower elevation), drier north-facing slopes while native richness tended to be higher on cooler (higher elevation) sites on south-facing slopes, with both alien and native richness higher at intermediate soil pH and distant from streams. Alien richness was low, and native richness was high, when there was a greater number of tree species per plot. The major difference was that, having controlled for other factors in the model, native and alien richness were positively associated in alien-dominated plots (increasing the total variation accounted for from 14% to 21% respectively), but negatively

Table 1 Parameter estimates from multiple regression models [generalized least squares (GLS) with spatial correlation structures] predicting native and alien species richness within: (i) all plots (d.f. = 1227), (ii) alien-dominated plots (d.f. = 739), and (iii) native-dominated plots (d.f. = 488) with climate, environmental and human-related explanatory variables

	All plots		Alien-dominated plots		Native-dominated plots	
Variables	Alien richness	Native richness	Alien richness	Native richness	Alien richness	Native richness
Total *N*	311	368	282	217	194	345
Mean *N*	16.4 ± 0.19	7.9 ± 0.23	17.5 ± 0.19	3.9 ± 0.15	14.7 ± 0.36	14.1 ± 0.4
Growing degree days	**3.39*****	**−2.99*****	2.01	**−2.61****	**3.11*****	**−5.26*****
Solar radiation	**0.87*****	**−1.44*****	0.04	**−0.86****	**1.28*****	**−2.12*****
Distance to buildings	−0.06	0.08	**−0.25****	**0.21***	0.11	−0.16
Distance to unpaved roads	0.09	**0.15****	−0.11	**0.17****	**0.15***	0.05
Distance to streams	**0.14****	−0.06	**0.21***	**0.21***	**0.17***	**−0.22****
Proportion tree/plot	**−0.33*****	**0.59*****	**−0.32*****	**0.29*****	**−0.61*****	**0.62*****
Soil pH	**1.96*****	**1.62*****	**2.05*****	**1.02***	1.25	**1.67***
Soil pH^2	**−1.28*****	**−1.05*****	**−1.34*****	**−0.65***	−0.83	**−1.08***
Alien richness	NA	**−0.58*****	NA	**1.41*****	NA	**−0.49*****
Native richness	**−0.18*****	NA	**0.75*****	NA	**−0.72*****	NA
R^2	0.11	0.23	0.14	0.21	0.19	0.25
Spatial correlation structures	Spherical	Exponential	Exponential	Spherical	Exponential	Gaussian

In all cases, the explanatory and response variables were transformed [log10(x + 1)] to ensure normality and to deal with zero values. Explanatory variables were then standardized to zero mean and standard deviation one so that parameter estimates were comparable. All explanatory variables (see Methods), were tested but only those variables that were statistically significant in at least one model are shown. Significant variables in a given model are shown in bold (***$P < 0.0001$, **$P < 0.001$, *$P < 0.05$). Also shown are the coefficients of determination (R^2), the total number of alien and native species (total *N*), and the mean number of native and alien species per plot (Mean *N*) (±SE).

associated in native-dominated plots (19% to 25% of total variation accounted for). In addition, alien richness increased and native richness declined significantly with proximity to buildings in alien-dominated plots and with distance to streams in native-dominated plots.

Alien species richness was generally higher than native species per plot across the elevation gradient (Table 2). However, native species richness increased with elevation for all plots and for plots dominated by either native or alien species, such that the only occasion mean native richness was greater than alien richness was at the highest elevations (> 400 m a.s.l.) within native-dominated plots. In contrast, alien species richness was less influenced by elevation and appears to have a unimodal relationship with a slight peak at mid elevations (Table 2). Across all plots, native and alien richness were significantly and positively associated up to 200 m a.s.l., but this relationship became increasingly negative at higher elevations, becoming significantly so above 400 m a.s.l. (Fig. 2). Splitting the analysis into alien- and native-dominated plots separately revealed that this trend reflects the positive relationship between native and alien richness in alien-dominated plots below 300 m a.s.l. and the negative relationship in native-dominated plots above 300 m a.s.l. Within each elevational band and across the entire elevation gradient, there was a consistent positive relationship between native and alien species richness in alien-dominated plots, and a consistent negative relationship in native-dominated plots (Fig. 2).

DISCUSSION

Previous interpretation of the sign and magnitude of the relationship between native and alien species richness has largely centred on the 'invasion paradox' that addresses how the shape and strength of the native–alien richness relationship can change with spatial grain and extent (Levine & D'Antonio, 1999; Shea & Chesson, 2002; Fridley *et al.*, 2004; Herben *et al.*, 2004). We show, however, that at a constant grain and extent, the relationship between native and alien richness differs between plant communities subject to relatively high or low human impact that are respectively dominated by either alien or native species. Such variation in the native–alien richness relationship at small plot sizes has previously been attributed to statistical problems associated with high turnover of species leading to high variation in species richness among plots and thus inconsistent relationships (Stohlgren *et al.*, 1999, 2006; Fridley *et al.*, 2007). Our data do show high among-plot variation in both native and alien richness (Fig. 1), but we nevertheless find highly significant relationships with the sign of that relationship shifting from positive to negative in going from alien- to native-dominated plots. This shift could not be fully explained by changes in any of the environmental, climatic or human variables that we measured, although the explanatory variables did a consistently better job explaining native than alien richness. This might be expected if aliens were reasonably ubiquitous as a result of human impacts. Indeed, unlike other studies

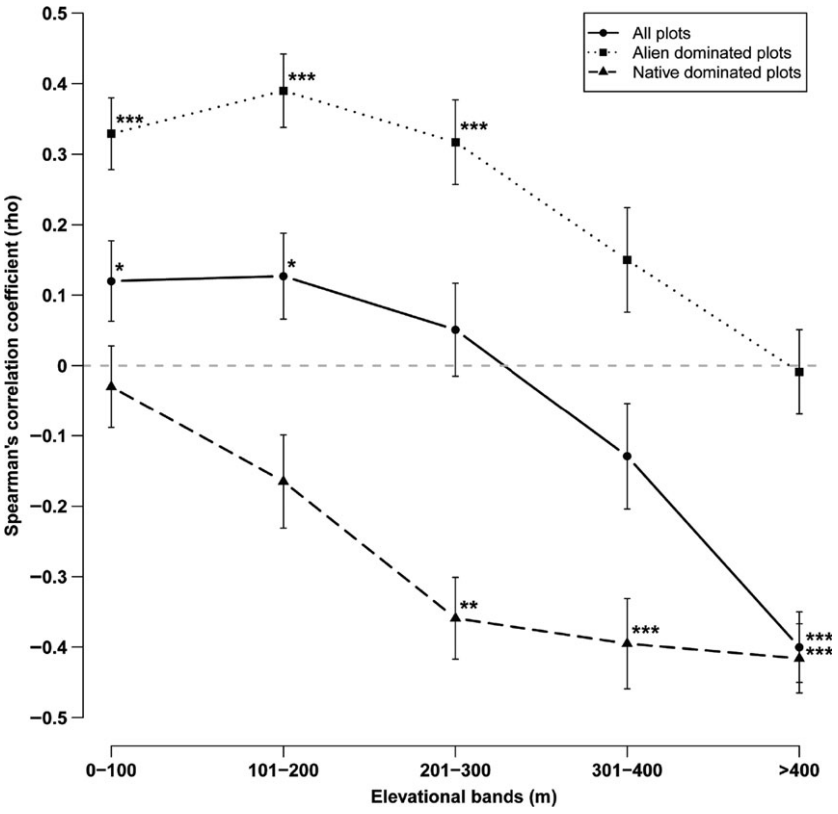

Figure 2 Change in Spearman's rank correlation coefficients (black dots with 95% confidence intervals) of native versus alien species richness within five elevational bands (0–100, 101–200, 201–300, 301–400 and > 400 m a.s.l.). Solid line shows native–alien relationship within all plots (n = 1227). Dotted line shows native–alien relationship within alien-dominated plots (n = 739). Broken line shows native–alien relationship within native-dominated plots (n = 488). The horizontal dotted line shows value of ρ = 0. The superscript refers to the statistical significance of correlations (***P < 0.001, **P < 0.01, *P < 0.05).

Table 2 Total number of alien and native species and mean number of species per plot within: all plots, alien-dominated and native-dominated plots in each separate elevational band. Total number of plots in each elevational band are shown

Elevational bands (m)	0–100		101–200		201–300		301–400		> 400	
	Alien	Native	Alien	Native	Alien	Native	Alien	Native	Alien	Native
All plots										
Tot. species	292	220	256	237	218	191	168	156	265	261
Mean species/plot	16.2	4.7	17.7	7.4	17.2	7.3	16.7	8.5	14.5	12.1
Tot. plots	296		260		223		172		276	
Alien-dominated plots										
Tot. species	219	143	154	131	146	114	97	81	123	108
Mean species/plot	17.0	2.5	18.1	4.1	17.9	3.5	17.5	4.1	16.9	6.3
Tot. plots	219		154		146		97		123	
Native-dominated plots										
Tot. species	68	73	100	105	67	76	69	75	135	151
Mean species/plot	13.1	11.0	16.9	12.3	15.8	14.4	15.7	14.2	12.6	16.7
Tot. plots	77		106		77		75		153	

that typically find a marked decline in alien richness with increasing elevation (Alexander *et al.*, 2011; Marini *et al.*, 2011, 2012), we observed relatively little change (Table 2). Grasslands across the entire elevation range, for example, tended to contain a similar suite of common alien species (e.g. *Lolium perenne*, *Dactylis glomerata* and *Anthoxanthum odoratum*).

Within native-dominated plots, the gradient of increasing native species richness coincided with a shift from plots at warmer, lower elevation on northerly aspects to plots at cooler and higher elevation sites on south-facing aspects, with a correspondingly greater proportion of trees. This gradient most likely reflects a legacy of past land-use, with less-modified or regenerating areas of native forest and shrubland occurring in less-accessible and less-productive higher-elevation south-facing sites, while mid-elevation warmer sites tend to support more modified native-dominated grassland.

Why then is alien species richness negatively correlated with native species richness along this gradient? The traditional interpretation would be that high native richness drives the

sign of the relationship and confers resistance to invasion by alien species (biotic resistance). However, while alien species richness declines along this gradient, plots with high native richness still have, on average, a high proportion of alien species (about one-half to one-third of species), suggesting that these sites are readily invaded. Instead, it may not be high native richness *per se* that confers resistance to invasion, but the fact that higher native richness coincides with a shift from grassland to remnant or regenerating native forest and shrubland. The understory of plots dominated by native woody vegetation may be less susceptible to invasion by alien grass or herbaceous species better adapted to more open environments, which comprise the bulk of the alien flora. The lower number of alien species and the higher number of native species in these native-dominated communities may thus reflect a shift in vegetation structure, from grassland to shrubland/forest, rather than being a function of biotic resistance linked with the number of species. Forested plots with high alien richness may also be in areas regenerating after agricultural abandonment, highlighting the potential for historical factors such as land-use change to influence current native–alien plant relationships (Parker *et al.*, 2010).

For alien-dominated plots, we see a positive association between native and alien species richness, which is commonly attributed to both native and alien species responding in a similar manner to underlying environmental gradients associated with plant performance (Gilbert & Lechowicz, 2005; Richardson *et al.*, 2005). However, in our study, only one variable (soil pH) appeared to influence native and alien richness similarly (Table 1). None of the remaining environmental variables we measured could fully explain the covariance between native and alien species richness. Thus, is there any evidence that native and alien species richness covary along either anthropogenic or climate gradients?

Stratifying by elevation helps disentangle the potentially confounding effects of covariance among anthropogenic and environmental variables (Marini *et al.*, 2012). The relationship between native and alien species richness was consistently positive or negative for alien-dominated and native-dominated plots, respectively, even when the variation in climate was constrained within fixed elevational bands. This suggests that anthropogenic effects shape these relationships more strongly than climate. Nevertheless, the strength of the positive and negative relationships changed with elevation, suggesting that the magnitude of anthropogenic effects also vary with elevation.

In contrast to the findings of Boughton *et al.* (2011) who found management intensity resulted in negative relationships between native and alien species, we interpreted our positive relationship to be a function of the intensity of management. Sites with low native and alien species richness are dominated by alien pasture grasses that are intensively managed through grazing, ploughing and fertilizer application to favour just a few highly productive fast growing alien species (for example *Lolium perenne* and *Trifolium* spp. swards). Less intensive management may allow pastures to be invaded by other alien and native species, leading to a positive relationship between the two, although aliens dominate in these more intensively managed systems. Thus, the positive relationship is driven by patterns in the persistence of native species along a gradient of management intensity that influences alien species richness to a much lesser extent.

With increasing elevation, climate variables might be expected to exert a greater influence on native and alien plant distributions and to affect these in a similar manner (Stohlgren *et al.*, 1999; Marini *et al.*, 2009; Pauchard *et al.*, 2009). However, across the large elevation gradient, while alien species richness showed a unimodal relationship that could be attributed to higher elevations becoming increasingly inclement, native richness progressively increased with elevation. While we might have expected a similar unimodal relationship for native species (Marini *et al.*, 2012), the linear relationship undoubtedly reflects the fact that much of the native diversity has been removed by forest clearance at low to mid elevations (Wilson, 2009). The outcome is that at low elevation, where most plots are heavily modified and dominated by alien species, native and alien richness are positively correlated, while at higher elevations, there is stronger spatial segregation and hence a negative correlation, with less-modified remnants of native forest vegetation tending to have more native and fewer alien species.

CONCLUSION

Much of the discussion to date regarding the drivers of native and alien species richness suffers from the fact that the grain and extent of studies are rarely independent and the grain size covaries with the spatial extent examined (Hulme, 2008). This prevents adequate assessment of the local and regional drivers on patterns of species richness. Our study is one of the few that examines patterns of species richness at a relatively fine grain (36 m^2) over a large spatial extent (*c.* 1000 km^2) (c.f. Stohlgren *et al.*, 2006; Chen *et al.*, 2010). Our results do not provide strong evidence of biotic resistance associated with higher native species richness limiting alien plant invasions, although this might only be expected to be found at even finer grain sizes (Levine & D'Antonio, 1999; Herben *et al.*, 2004). In contrast, our study confirms an increasing and recent body of evidence (Parker *et al.*, 2010; Boughton *et al.*, 2011) that indicates contemporary and historical anthropogenic impacts strongly shape both negative and positive relationships between native and alien species richness, especially where such impacts covary with climate gradients. The impact of local management effects (e.g. land clearance, grazing) may be less discernible at larger grain sizes (> 1 km^2) where other broad-scale environmental factors are likely to shape patterns in species richness.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Schematic map of Banks Peninsula (c. 1000 Km^2), its location in New Zealand (inset) and details of the vegetation sampling design.

Table S1 Characteristics of 18 explanatory variables calculated for each of 1227 plots in the Banks Peninsula study area, and used in the analyses.

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BIOSKETCHES

Federico Tomasetto has broad interests in ecology, GIS and remote sensing analysis with a current focus on invasion ecology. This work is part of his PhD thesis under the supervision of Richard P. Duncan and Philip E. Hulme at the Bio-Protection Research Centre, Lincoln University.

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Author contributions: F.T., R.P.D. and P.E.H conceived the ideas; F.T. collected the data; F.T. analysed the data with advice from R.P.D. and P.E.H. All authors contributed to the writing of the manuscript.

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Appendix L

List of studies for the global meta-analysis on native-alien plant species richness relationship

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Appendix M

Cleveland dot plot of the mean effect size for five different datasets

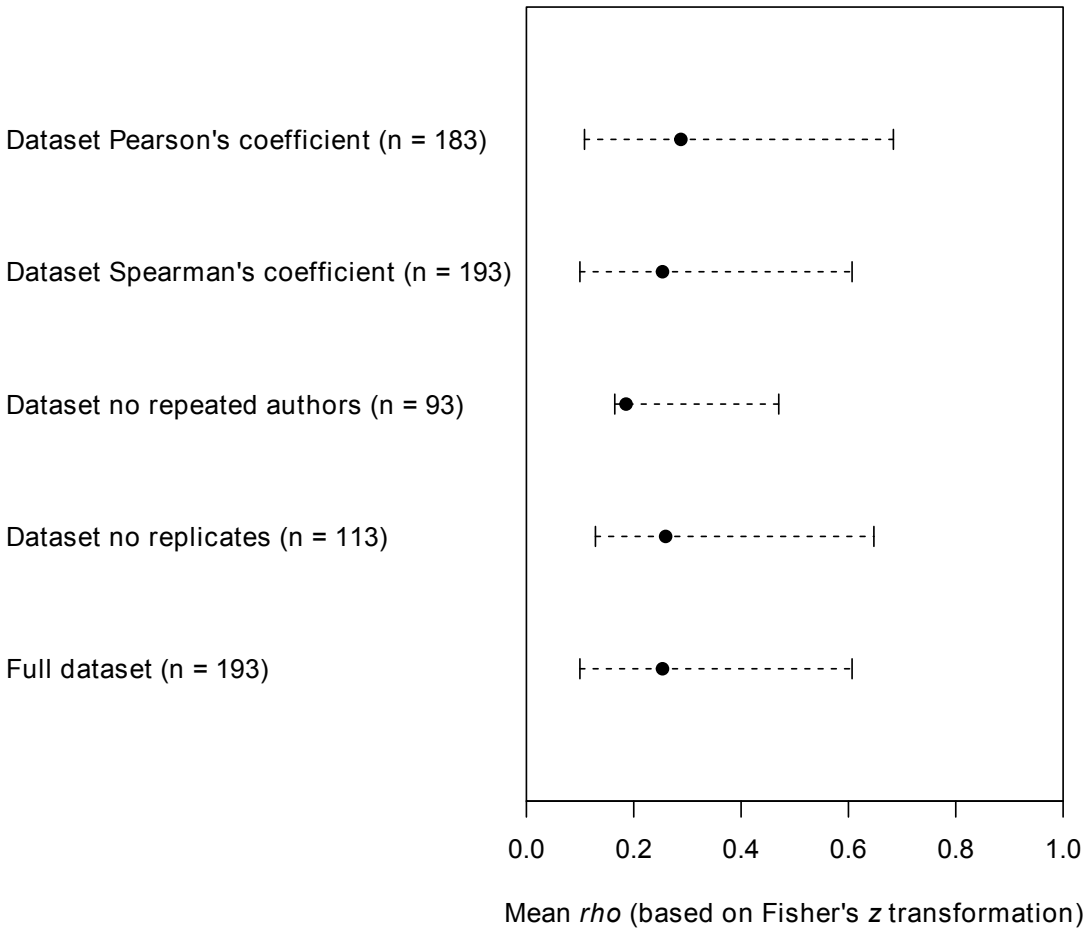

Figure M.1. Cleveland dot plot of the mean effect size (correlation coefficient based on the Fisher's z transformation) from randomly selected effect sizes ($n = 10000$ permutations) with 95%-CI for five different datasets: all case studies (full dataset), only one study per article (dataset no replicates), only one study per author (dataset no repeated authors), studies using Spearman correlation coefficient (*rho*; dataset Spearman's coefficient) and studies using Pearson's correlation coefficient (r; dataset Pearson's coefficient).

Appendix N

Funnel plot of effect sizes

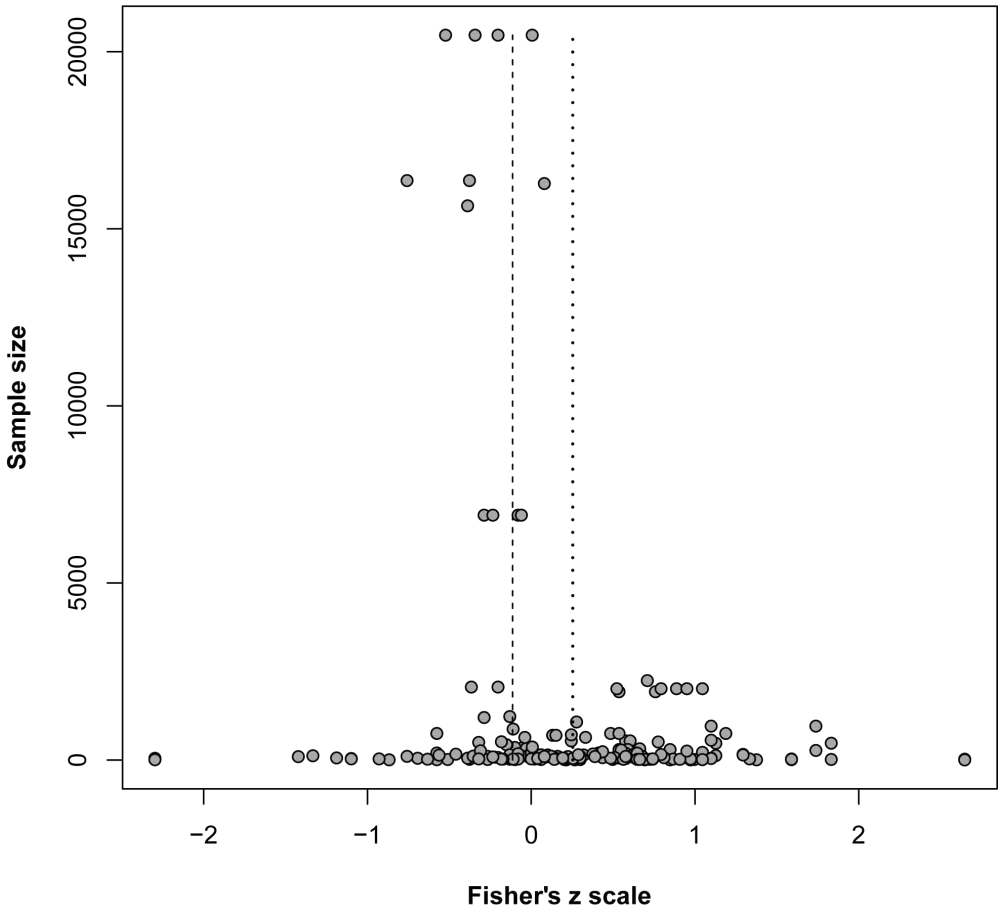

Figure N.1. Funnel plot of effect sizes (Fisher's z) of the raw data versus sample size. The vertical dashed line shows value of the mean effect size from the fixed effect model. The vertical dotted line shows the mean effect size from the random effect model.

Appendix O

The relationships between NARR and five significant moderators

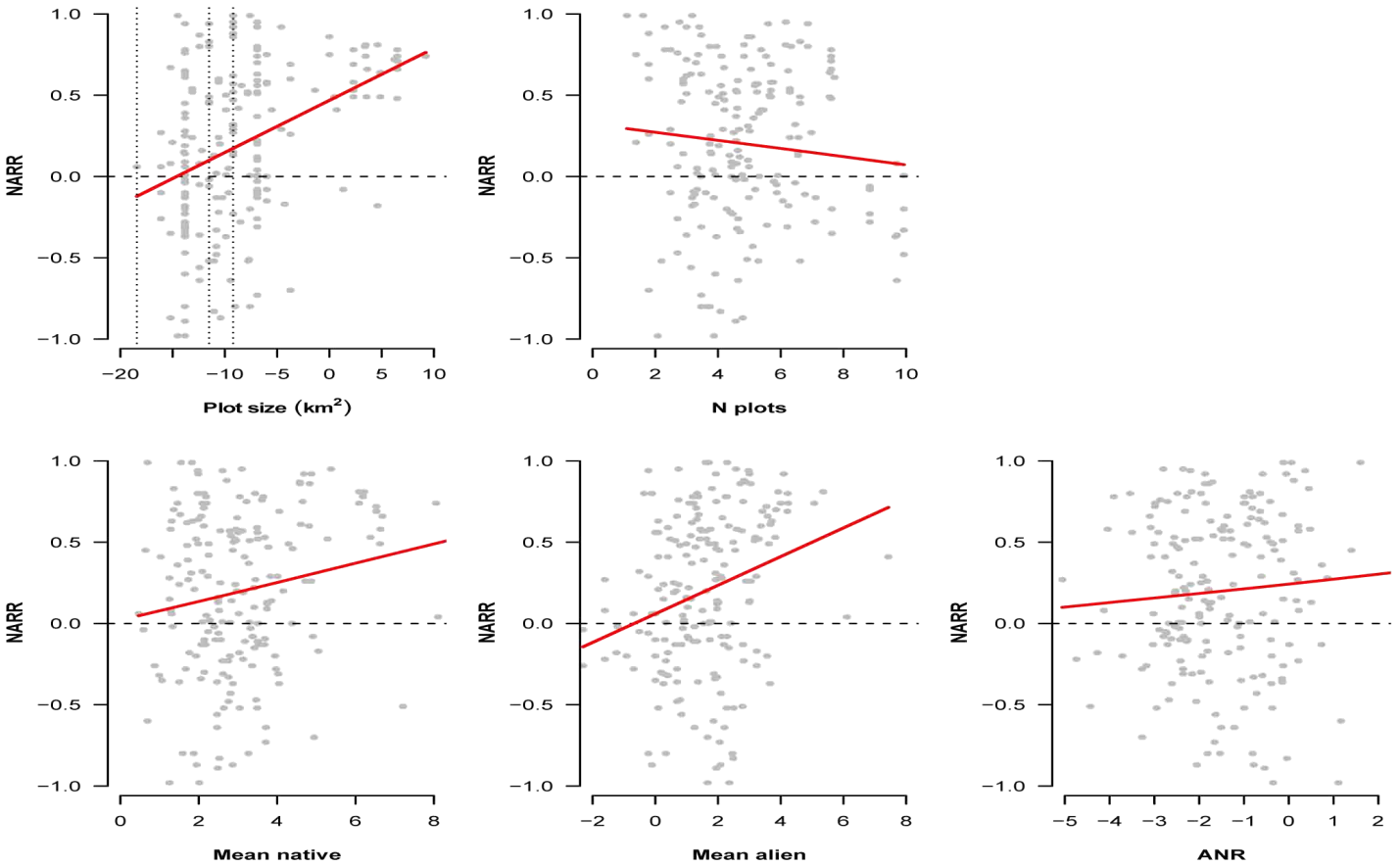

Figure O.1. The relationships between native-alien species richness relationship (NARR; back-transformed effect size z) and five significant moderators ($P < 0.001$; Table 5.1). NARR was consistently positively correlated with plot size ($rho = 0.36$, d.f. $= 191$, $P < 0.001$), mean alien ($rho = 0.27$, d.f. $= 191$, $P < 0.001$), mean native ($rho = 0.13$, d.f. $= 191$, $P < 0.05$) and ANR ($rho = 0.42$, d.f. $= 191$, $P < 0.001$), but negatively and not significantly correlated with number of plots ($rho =$ -0.07, d.f. $= 191$, n.s.). In all cases, logarithmic scale of the x-axis is shown. Grey points are individual case study. The horizontal dotted line shows value of NARR = 0. The vertical dotted line shows three different sub-groups of plot sizes (see Methods). Solid lines show a linear regression fitted to the full data set.

Appendix P

Total heterogeneity all studies and sub-groups plot size

Table P.1. Mean effect size (Fisher's *z* transformation) with *P*-values in the native-alien species richness relationship between: all studies and different groups of plot sizes. Total heterogeneity (*Qt*) with indication of *P*-values and the ratio of true heterogeneity to total observed variation [I^2; Higgins *et al.* (2003)] are shown. Weighted linear regression of the treatment effect on its standard error (i.e. Egger's test) and *P*-values related are also shown. Significant values of mean effect size are shown in bold. See text for a detailed description of statistical analysis.

Levels	Sub-groups	Effect size	CI (lb)	CI (ub)	*P*-values	*Q*	*P*-values	I^2 *(%)*	Egger's test	*P*(t) Egger
All studies	-	**0.26**	0.16	0.35	< 0.001	48924.9	< 0.001	99.6	1.16	n.s.
	0 - 10 m^2	0.07	-0.1	0.25	n.s.	20678	<0.001	99.7	-1.03	n.s.
Studies by plot size	**11 - 100 m^2**	0.18	-0.03	0.38	n.s.	5761.55	< 0.001	99.3	0.06	n.s.
	> 100 m^2	**0.42**	0.3	0.53	< 0.001	13775	< 0.001	99.4	**2.39**	**< 0.05**

Appendix Q

Full list of plant species on Banks Peninsula

Table Q.1. Complete list of the native and alien vascular plant species encountered in Banks Peninsula floristic survey (1983−1988). Species names with the superscript refers to the plant species status (** Alien). Growth forms: FE) Fern; GR) Grass; HR) Herb; SH) Shrub; TR) Tree. Species occurrence.

Family	Species	Growth forms	Sp.occurence
Fabaceae	*Acacia aneura* F. Muell.**	SH	4
Fabaceae	*Acacia dealbata* Link**	SH	1
Fabaceae	*Acacia mearnsii* De Wild.**	TR	1
Rosaceae	*Acaena agnipila* Gand.**	HR	25
Rosaceae	*Acaena anserinifolia* (J.R.Forst. & G.Forst.) J.B.Armstr.	HR	96
Rosaceae	*Acaena caesiiglauca* (Bitter) Bergmans	HR	3
Rosaceae	*Acaena dumicola* B.H.Macmill.	HR	2
Rosaceae	*Acaena juvenca* B.H.Macmill.	HR	3
Rosaceae	*Acaena novae-zelandiae* Kirk	HR	49
Rosaceae	*Acaena* spp. L.	HR	3
Sapindaceae	*Acer pseudoplatanus* L.**	TR	7
Asteraceae	*Achillea millefolium* L.**	HR	299
Apiaceae	*Aciphylla aurea* W.R.B.Oliv.	HR	2
Apiaceae	*Aciphylla subflabellata* W.R.B.Oliv.	HR	13
Epacridaceae	*Acrothamnus colensoi* (Hook.f.) Quinn	SH	2
Alliaceae	*Agapanthus praecox* subsp. *orientalis* (F.M.Leight.) F.M.Leight.**	HR	1
Poaceae	*Agrostis capillaris* L.**	GR	458
Poaceae	*Agrostis gigantea* Roth**	GR	3
Poaceae	*Agrostis muelleriana* Vickery	GR	1

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Family	Species	Growth forms	Sp.occurence
Poaceae	*Agrostis stolonifera* L.**	GR	75
Poaceae	*Aira caryophyllea* L.**	GR	175
Poaceae	*Aira praecox* L.**	GR	2
Sapindaceae	*Alectryon excelsus* Gaertn.	TR	9
Poaceae	*Alopecurus geniculatus* L.**	GR	10
Amaranthaceae	*Amaranthus deflexus* L.**	HR	3
Amaranthaceae	*Amaranthus powellii* S.Watson**	HR	3
Primulaceae	*Anagallis arvensis* L.**	HR	26
Asteraceae	*Anaphalioides bellidioides* (G.Forst.) Glenny	HR	60
Apiaceae	*Anisotome aromatica* Hook.f.	HR	3
Pteridaceae	*Anogramma leptophylla* (L.) Link	FE	4
Asteraceae	*Anthemis cotula* L.**	HR	2
Poaceae	*Anthoxanthum odoratum* L.**	GR	867
Apiaceae	*Anthriscus caucalis* M.Bieb.**	HR	29
Rosaceae	*Aphanes arvensis* L.**	HR	122
Rosaceae	*Aphanes inexspectata* W.Lippert**	HR	51
Rosaceae	*Aphanes* spp. L.**	HR	2
Apiaceae	*Apium prostratum* Labill. ex Vent.	HR	1
Asteraceae	*Arctotheca calendula* (L.) Levyns**	HR	3
Asteraceae	*Arctotis* spp. L.**	HR	3
Caryophyllaceae	*Arenaria serpyllifolia* L.**	HR	18
Elaeocarpaceae	*Aristotelia serrata* (J.R.Forst. & G.Forst.) W.R.B.Oliv.	TR	12

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Family	Species	Growth forms	Sp.occurence
Poaceae	*Arrhenatherum elatius* (L.) J.Presl & C.Presl**	GR	47
Anthericaceae	*Arthropodium candidum* Raoul	GR	20
Aspleniaceae	*Asplenium appendiculatum* (Labill.) C. Presl	FE	82
Aspleniaceae	*Asplenium bulbiferum* G.Forst.	FE	61
Aspleniaceae	*Asplenium flabellifolium* Cav.	FE	173
Aspleniaceae	*Asplenium flaccidum* G.Forst.	FE	14
Aspleniaceae	*Asplenium gracillimum* Colenso	FE	27
Aspleniaceae	*Asplenium hookerianum* Colenso	FE	114
Aspleniaceae	*Asplenium oblongifolium* Colenso	FE	5
Aspleniaceae	*Asplenium richardii* (Hook.f.) Hook.f.	FE	1
Asteliaceae	*Astelia fragrans Colenso*	HR	14
Chenopodiaceae	*Atriplex prostrata Boucher* ex DC.**	HR	1
Poaceae	*Austrostipa nodosa* (S.T.Blake) S.W.L.Jacobs & J.Everett**	GR	23
Poaceae	*Avena fatua* L.**	GR	4
Asteraceae	*Bellis perennis* L.**	HR	184
Berberidaceae	*Berberis glaucocarpa* Stapf**	SH	3
Blechnaceae	*Blechnum blechnoides* (Bory) Keyserl.	FE	1
Blechnaceae	*Blechnum chambersii* L.	FE	39
Blechnaceae	*Blechnum colensoi* (Hook.f. in Hook.) N.A.Wakef.	FE	2
Blechnaceae	*Blechnum discolor* (G.Forst.) Keyserl.	FE	12
Blechnaceae	*Blechnum fluviatile* (R.Br.) Lowe ex Salomon	FE	60
Blechnaceae	*Blechnum minus* (R.Br.) Ettingsh.	FE	6

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Family	Species	Growth forms	Sp.occurence
Blechnaceae	*Blechnum montanum* T.C.Chambers & P.A.Farrant	FE	1
Blechnaceae	*Blechnum novae-zelandiae* T.C.Chambers & P.A.Farrant	FE	1
Blechnaceae	*Blechnum penna-marina* (Poir.) Kuhn	FE	19
Blechnaceae	*Blechnum penna-marina* subsp. *alpina* T.C.Chambers & P.A.Farrant (1996)	FE	1
Blechnaceae	*Blechnum procerum* (G.Forst.) Sw.	FE	20
Blechnaceae	*Blechnum* spp. L.	FE	2
Blechnaceae	*Blechnum vulcanicum* (Blume) Kuhn	FE	1
Asteraceae	*Brachyglottis lagopus* (Raoul) B.Nord.	GR	8
Asteraceae	*Brachyglottis sciadophila* (Raoul) B.Nord.	SH	4
Brassicaceae	*Brassica oleracea* L.**	HR	2
Brassicaceae	*Brassica rapa* L.**	HR	1
Brassicaceae	*Brassica rapa* subsp. *sylvestris* (L.) Janch.**	HR	1
Poaceae	*Briza minor* L.**	GR	5
Poaceae	*Bromus catharticus* Vahl**	GR	1
Poaceae	*Bromus diandrus* Roth**	GR	104
Poaceae	*Bromus hordeaceus* L.**	GR	594
Poaceae	*Bromus lithobius* Trin.**	GR	25
Poaceae	*Bromus sitchensis* Trin.**	GR	8
Poaceae	*Bromus* spp. Scop.**	GR	3
Poaceae	*Bromus stamineus* E.Desv.**	GR	13
Poaceae	*Bromus sterilis* L.**	GR	21
Poaceae	*Bromus willdenowii* Kunth**	GR	24

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Family	Species	Growth forms	Sp.occurence
Apiaceae	*Bupleurum tenuissimum* L.**	HR	1
Portulacaceae	*Calandrinia menziesii* (Hook.) Torr. & A.Gray**	HR	1
Callitrichaceae	*Callitriche stagnalis* Scop.**	SH	12
Convolvulaceae	*Calystegia silvatica* (Kit.) Griseb.**	SH	1
Convolvulaceae	*Calystegia tuguriorum* (G.Forst.) R.Br. ex Hook.f.	SH	91
Brassicaceae	*Capsella bursa-pastoris* (L.) Medik.**	HR	33
Brassicaceae	*Cardamine debilis* Banks ex DC.	HR	89
Brassicaceae	*Cardamine hirsuta* L.	HR	24
Brassicaceae	*Cardamine* spp. L.	HR	1
Asteraceae	*Carduus pycnocephalus* L.**	HR	274
Asteraceae	*Carduus* spp. L.**	HR	1
Asteraceae	*Carduus tenuiflorus* Curtis**	HR	41
Cyperaceae	*Carex breviculmis* R.Br.	HR	90
Cyperaceae	*Carex colensoi* Boott	HR	69
Cyperaceae	*Carex coriacea* Hamlin	HR	2
Cyperaceae	*Carex flaviformis* Nelmes	HR	1
Cyperaceae	*Carex forsteri* Wahlenb.	HR	5
Cyperaceae	*Carex geminata* Schkuhr	HR	4
Cyperaceae	*Carex inversa* R.Br.	HR	1
Cyperaceae	*Carex raoulii* Boott	HR	1
Cyperaceae	*Carex resectans* Cheeseman	HR	8
Cyperaceae	*Carex secta* Boott	HR	2

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Family	Species	Growth forms	Sp.occurence
Cyperaceae	*Carex virgata* Sol. ex Boott	HR	8
Cyperaceae	*Carex wakatipu* Petrie	HR	1
Fabaceae	*Carmichaelia australis* R.Br.	SH	34
Fabaceae	*Carmichaelia* spp. R.Br.	SH	1
Aizoaceae	*Carpobrotus edulis* (L.) N.E.Br.**	HR	1
Rousseaceae	*Carpodetus serratus* J.R.Forst. & G.Forst.	TR	31
Pinaceae	*Cedrus atlantica* (Endl.) Carrière**	TR	1
Asteraceae	*Celmisia gracilenta* Hook.f.	HR	1
Asteraceae	*Celmisia mackaui* Raoul	HR	1
Asteraceae	*Centaurea melitensis* L.**	HR	1
Gentianaceae	*Centaurium erythraea* Rafn.**	HR	16
Gentianaceae	*Centaurium* spp. Hill**	HR	1
Gentianaceae	*Centaurium tenuiflorum* (Hoffm. & Link) Fritsch ex Janch.**	HR	19
Apiaceae	*Centella uniflora* (Colenso) Nannf.	HR	8
Valerianaceae	*Centranthus ruber* (L.) DC.**	HR	3
Caryophyllaceae	*Cerastium fontanum* Baumg.**	HR	2
Caryophyllaceae	*Cerastium fontanum* subsp. *vulgare* (Hartm.) Greuter & Burdet**	HR	676
Caryophyllaceae	*Cerastium glomeratum* Thuill.**	HR	297
Caryophyllaceae	*Cerastium semidecandrum* L.**	HR	23
Apiaceae	*Chaerophyllum colensoi* (Hook.f.) K.F.Chung	HR	14
Apiaceae	*Chaerophyllum novae-zelandiae*	HR	2
Apiaceae	*Chaerophyllum ramosum* (Hook.f.) K.F.Chung	HR	4

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Family	Species	Growth forms	Sp.occurence
Fabaceae	*Chamaecytisus palmensis* (H.Christ) F.A.Bisby & K.W.Nicholls**	TR	3
Pteridaceae	*Cheilanthes distans* (R.Br.) Mett.	FE	8
Pteridaceae	*Cheilanthes sieberi* Kunze in Lehm.	FE	8
Amaranthaceae	*Chenopodium album* L.**	HR	15
Amaranthaceae	*Chenopodium murale* L.**	HR	2
Poaceae	*Chionochloa conspicua* (G.Forst.) Zotov	GR	1
Poaceae	*Chionochloa rigida* (Raoul) Zotov	GR	13
Asteraceae	*Chrysanthemoides monilifera* (L.) Norl.**	SH	4
Asteraceae	*Cirsium arvense* (L.) Scop.**	HR	161
Asteraceae	*Cirsium vulgare* (Savi) Ten.**	HR	603
Portulacaceae	*Claytonia perfoliata* Donn ex Willd.**	HR	10
Ranunculaceae	*Clematis afoliata* Buchanan	SH	2
Ranunculaceae	*Clematis foetida* Raoul	SH	69
Ranunculaceae	*Clematis paniculata* J.F.Gmel.	SH	9
Ranunculaceae	*Clematis vitalba* L.**	SH	3
Lamiaceae	*Clinopodium vulgare* L.**	HR	8
Rutaceae	*Coleonema pulchrum* Hook.**	TR	1
Caryophyllaceae	*Colobanthus strictus* Cheeseman	HR	2
Apiaceae	*Conium maculatum* L.**	HR	9
Convolvulaceae	*Convolvulus waitaha* (Sykes) Heenan, Molloy & de Lange	SH	44
Asteraceae	*Conyza bonariensis* (L.) Cronquist**	HR	1
Asteraceae	*Conyza sumatrensis* (Retz.) E.H.Walker**	HR	6

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Family	Species	Growth forms	Sp.occurence
Rubiaceae	*Coprosma areolata* Cheeseman	SH	32
Rubiaceae	*Coprosma ciliata* Hook.f.	SH	13
Rubiaceae	*Coprosma crassifolia* Colenso	SH	117
Rubiaceae	*Coprosma dumosa* (Cheeseman) G.T.Jane	TR	85
Rubiaceae	*Coprosma linariifolia* Hook.f.	TR	8
Rubiaceae	*Coprosma lucida* J.R.Forst. & G.Forst.	SH	14
Rubiaceae	*Coprosma obconica* Kirk	SH	1
Rubiaceae	*Coprosma propinqua* A.Cunn.	SH	73
Rubiaceae	*Coprosma repens* A.Rich.	TR	2
Rubiaceae	*Coprosma rhamnoides* A.Cunn.	SH	183
Rubiaceae	*Coprosma rigida* Cheeseman	SH	48
Rubiaceae	*Coprosma robusta* Raoul	SH	43
Rubiaceae	*Coprosma rotundifolia* A.Cunn.	SH	133
Rubiaceae	*Coprosma rubra* Petrie	SH	9
Rubiaceae	*Coprosma* spp. J.R.Forster & G.Forster	SH	4
Rubiaceae	*Coprosma virescens* Petrie	SH	49
Rubiaceae	*Coprosma wallii* Petrie in Cheeseman	SH	1
Laxmanniaceae	*Cordyline australis* (G.Forst.) Endl.	TR	5
Coriariaceae	*Coriaria arborea* Linds.	TR	2
Coriariaceae	*Coriaria sarmentosa* G.Forst.	SH	3
Argophyllaceae	*Corokia cotoneaster* Raoul	SH	15
Poaceae	*Cortaderia richardii* (Endl.) Zotov	GR	4

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Family	Species	Growth forms	Sp.occurence
Poaceae	*Cortaderia selloana* (Schult. & Schult.f.) Asch. & Graebn.**	GR	1
Myrtaceae	*Corymbia ficifolia* (F.Muell.) K.D.Hill & L.A.S.Johnson**	TR	1
Rosaceae	*Cotoneaster* spp. Medik.**	SH	1
Asteraceae	*Cotula australis* (Spreng.) Hook.f.	HR	67
Asteraceae	*Cotula coronopifolia* L.	HR	3
Crassulaceae	*Cotyledon orbiculata* L.**	SH	6
Asteraceae	*Craspedia minor* (Hook.f.) Allan	HR	11
Crassulaceae	*Crassula sieberiana* (Schult. & Schult.f.) Druce	HR	92
Rosaceae	*Crataegus monogyna* Jacq.**	TR	12
Asteraceae	*Crepis capillaris* (L.) Wallr.**	HR	802
Asteraceae	*Crepis vesicaria* L.**	HR	22
Poaceae	*Critesion hystrix* (Roth) Á.L'ove**	GR	2
Poaceae	*Critesion marinum* (Huds) Á.L'ove**	GR	9
Poaceae	*Critesion murinum* (L.) Á.L'ove **	GR	159
Poaceae	*Critesion murinum* subsp. *leporinum* (Link) Á.L'ove**	GR	1
Grammitidiaceae	*Ctenopteris heterophylla* (Labill.) Tindale	FE	2
Cupressaceae	*Cupressus macrocarpa* Hartw. ex Gordon**	TR	8
Cupressaceae	*Cupressus sempervirens* L.**	TR	1
Cyatheaceae	*Cyathea colensoi* (Hook.f.) Domin	FE	2
Cyatheaceae	*Cyathea dealbata* (G.Forst.) Sw.	FE	11
Cyatheaceae	*Cyathea smithii* Hook.f.	FE	4
Poaceae	*Cynosurus cristatus* L.**	GR	736

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Family	Species	Growth forms	Sp.occurence
Poaceae	*Cynosurus echinatus* L.**	GR	98
Fabaceae	*Cytisus scoparius* (L.) Link**	SH	40
Podocarpaceae	*Dacrycarpus dacrydioides* (A.Rich.) de Laub.	TR	1
Poaceae	*Dactylis glomerata* L.**	GR	956
Apiaceae	*Daucus glochidiatus* (Labill.) Fisch., C.A.Mey. & Avé-Lall.	HR	15
Poaceae	*Deyeuxia avenoides* (Hook.f.) Buchanan	GR	15
Caryophyllaceae	*Dianthus armeria* L.**	HR	9
Caryophyllaceae	*Dianthus* spp. L.**	HR	1
Poaceae	*Dichelachne crinita* (L.f.) Hook.f.	GR	93
Convolvulaceae	*Dichondra brevifolia* Buchanan	HR	5
Convolvulaceae	*Dichondra repens* J.R.Forst. & G.Forst.	HR	194
Dicksoniaceae	*Dicksonia squarrosa* (G.Forst.) Sw.	FE	6
Ericaceae	*Digitalis purpurea* L.**	HR	246
Brassicaceae	*Diplotaxis muralis* (L.) DC.**	HR	1
Rhamnaceae	*Discaria toumatou* Raoul	SH	26
Aizoaceae	*Disphyma australe* (W.T.Aiton) N.E.Br.	HR	8
Sapindaceae	*Dodonaea viscosa* Jacq.	TR	3
Ericaceae	*Dracophyllum acerosum* Berggr.	SH	6
Dryopteridaceae	*Dryopteris filix-mas* (L.) Schott**	FE	1
Poaceae	*Echinopogon ovatus* (G.Forst.) P.Beauv.	GR	21
Boraginaceae	*Echium candicans* L.f.**	SH	1
Amaranthaceae	*Einadia allanii* (Aellen) Paul G.Wilson	HR	14

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Family	Species	Growth forms	Sp.occurence
Amaranthaceae	*Einadia triandra* (G.Forst.) A.J.Scott	HR	4
Cyperaceae	*Eleocharis acuta* R.Br.	GR	4
Poaceae	*Elymus rectisetus* (Nees) Á.L'ove & Connor**	GR	402
Poaceae	*Elytrigia repens* (L.) Nevski**	GR	17
Onagraceae	*Epilobium alsinoides* A.Cunn.	HR	3
Onagraceae	*Epilobium alsinoides* subsp. *atriplicifolium* (A.Cunn.) P.H.Raven & Engelhorn	HR	57
Onagraceae	*Epilobium billardierianum* Ser. ex DC. subsp. *cinereum* (A. Rich. in d'Urv.) P.H.Raven & Engelhorn	HR	4
Onagraceae	*Epilobium brunnescens* (Cockayne) P.H.Raven & Engelhorn subsp. *brunnescens*	HR	2
Onagraceae	*Epilobium ciliatum* Raf.**	HR	8
Onagraceae	*Epilobium insulare* Hausskn.	HR	1
Onagraceae	*Epilobium komarovianum* H.Lév.	HR	2
Onagraceae	*Epilobium nerteroides* A.Cunn.	HR	2
Onagraceae	*Epilobium nummulariifolium* A.Cunn.	HR	18
Onagraceae	*Epilobium pubens* A.Rich.	HR	28
Onagraceae	*Epilobium rotundifolium* G.Forst.	HR	3
Onagraceae	*Epilobium* spp. L.	HR	2
Geraniaceae	*Erodium cicutarium* (L.) L'Hér.**	HR	37
Geraniaceae	*Erodium moschatum* (L.) L'Hér.**	HR	52
Brassicaceae	*Erysimum cheiri* L.**	HR	1
Papaveraceae	*Eschscholzia californica* Cham.**	HR	2
Myrtaceae	*Eucalyptus globulus* Labill.**	TR	1

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Family	Species	Growth forms	Sp.occurence
Myrtaceae	*Eucalyptus obliqua* L'Hér.**	TR	1
Myrtaceae	*Eucalyptus* spp. L'Hér.**	TR	2
Myrtaceae	*Eucalyptus viminalis* Labill.**	TR	1
Asteraceae	*Euchiton audax* (D.G.Drury) Holub	HR	135
Asteraceae	*Euchiton involucratus* (G.Forst.) Holub	HR	5
Asteraceae	*Euchiton japonicus* (Thunb.) Holub	HR	23
Asteraceae	*Euchiton limosus* (D.G.Drury) Holub	HR	9
Asteraceae	*Euchiton sphaericus* (Willd.) Holub	HR	1
Asteraceae	*Euchiton* spp. L.	HR	1
Euphorbiaceae	*Euphorbia peplus* L.**	HR	12
Polygonaceae	*Fallopia convolvulus* (L.) Á.L'ove**	HR	2
Poaceae	*Festuca actae* Connor	GR	1
Poaceae	*Festuca novae-zelandiae* (Hack.) Cockayne	GR	70
Poaceae	*Festuca ovina* subsp. *hirtula* (W.G.Travis) M.J.Wilk.**	GR	11
Poaceae	*Festuca rubra* L. *subsp*. rubra**	GR	8
Poaceae	*Festuca rubra* subsp. *commutata* Gaudin**	GR	45
Poaceae	*Festuca* spp. L.	GR	2
Cyperaceae	*Ficinia nodosa* (Rottb.) Goetgh., Muasya & D.A.Simpson	HR	12
Apiaceae	*Foeniculum vulgare* Mill.**	HR	3
Oleaceae	*Forsythia* spp. Vahl**	SH	1
Onagraceae	*Fuchsia* ×*colensoi* Hook.f.	SH	9
Onagraceae	*Fuchsia excorticata* (J.R.Forst. & G.Forst.) L.f.	TR	102

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Family	Species	Growth forms	Sp.occurence
Onagraceae	*Fuchsia magellanica* Lam.**	SH	1
Onagraceae	*Fuchsia perscandens* Cockayne & Allan	SH	2
Papaveraceae	*Fumaria muralis* W.D.J.Koch**	HR	3
Rubiaceae	*Galium aparine* L.**	HR	155
Rubiaceae	*Galium divaricatum* Lam.**	HR	9
Rubiaceae	*Galium perpusillum* (Hook.f.) Allan	HR	1
Rubiaceae	*Galium propinquum* A.Cunn.	HR	26
Ericaceae	*Gaultheria antipoda* G.Forst.	SH	4
Ericaceae	*Gaultheria depressa* Hook.f.	SH	3
Ericaceae	*Gaultheria depressa* var. *novae-zelandiae* D.A.Franklin	SH	3
Asteraceae	*Gazania* spp. Gaertn.**	HR	1
Fabaceae	*Genista monspessulana* (L.) L.A.S.Johnson**	SH	1
Geraniaceae	*Geranium brevicaule* Hook.f.	HR	1
Geraniaceae	*Geranium microphyllum* Hook.f.	HR	92
Geraniaceae	*Geranium molle* L.**	HR	220
Geraniaceae	*Geranium pusillum* L.**	HR	1
Geraniaceae	*Geranium retrorsum* L'Hér. ex DC.	HR	2
Geraniaceae	*Geranium sessiliflorum* Cav.	HR	32
Geraniaceae	*Geranium solanderi* Carolin	HR	2
Apiaceae	*Gingidia enysii* var. *peninsulare* J.W.Dawson	HR	1
Poaceae	*Glyceria declinata* Bréb.**	GR	14
Grammitidiaceae	*Grammitis ciliata* Colenso	FE	1

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Family	Species	Growth forms	Sp.occurence
Griseliniaceae	*Griselinia littoralis* Raoul	TR	70
Gunneraceae	*Gunnera monoica* Raoul	HR	11
Haloragaceae	*Haloragis erecta* (Banks ex Murray) Oken	HR	14
Ericaceae	*Hebe salicifolia* (G.Forst.) Pennell	SH	29
Ericaceae	*Hebe strictissima* (Kirk) L.B.Moore	SH	10
Araliaceae	*Hedera helix* L.**	SH	1
Monimiaceae	*Hedycarya arborea* J.R.Forst. & G.Forst.	TR	22
Asteraceae	*Helichrysum filicaule* Hook.f.	HR	178
Asteraceae	*Helichrysum lanceolatum* (Buchanan) Kirk	HR	46
Ericaceae	*Heliohebe lavaudiana* (Raoul) Garn.-Jones	SH	2
Asteraceae	*Helminthotheca echioides* (L.) Holub**	HR	9
Asteraceae	*Hieracium lepidulum* (Stenstr.) Omang**	HR	2
Asteraceae	*Hieracium pilosella* L.**	HR	23
Asteraceae	*Hieracium praealtum* Gochnat**	HR	1
Poaceae	*Hierochloe redolens* (Vahl) Roem. & Schult.	GR	17
Brassicaceae	*Hirschfeldia incana* (L.) Lagr.-Foss.**	HR	1
Dennstaedtiaceae	*Histiopteris incisa* (Thunb.) J.Sm.	FE	2
Malvaceae	*Hoheria angustifolia* Raoul	TR	74
Malvaceae	*Hoheria populnea* A.Cunn.	TR	1
Poaceae	*Holcus lanatus* L.**	GR	902
Poaceae	*Hordeum* spp. L.**	GR	8
Poaceae	*Hordeum vulgare* subsp. *distichon* (L.) Körn.**	GR	5

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Family	Species	Growth forms	Sp.occurence
Lycopodiaceae	*Huperzia varia* (R.Br.) Trevis.	FE	2
Apiaceae	*Hydrocotyle americana* L.**	HR	3
Apiaceae	*Hydrocotyle elongata* A.Cunn.	HR	2
Apiaceae	*Hydrocotyle heteromeria* A.Rich.	HR	53
Apiaceae	*Hydrocotyle moschata* G.Forst.	HR	146
Apiaceae	*Hydrocotyle novae-zeelandiae* DC.	HR	4
Apiaceae	*Hydrocotyle novae-zeelandiae* var. *montana* Kirk	HR	131
Hymenophyllaceae	*Hymenophyllum rarum* R.Br.	FE	1
Clusiaceae	*Hypericum androsaemum* L.**	SH	1
Clusiaceae	*Hypericum involutum* (Labill.) Choisy	HR	4
Clusiaceae	*Hypericum pusillum* Choisy	HR	2
Asteraceae	*Hypochaeris glabra* L.**	HR	62
Asteraceae	*Hypochaeris radicata* L.**	HR	957
Dennstaedtiaceae	*Hypolepis ambigua* (A.Rich.) Brownsey & Chinnock	FE	10
Dennstaedtiaceae	*Hypolepis millefolium* Hook.	FE	4
Dennstaedtiaceae	*Hypolepis rufobarbata* (Colenso) N.A.Wakef.	FE	5
Loranthaceae	*Ileostylus micranthus* (Hook.f.) Tiegh.	SH	4
Iridaceae	*Iris foetidissima* L.**	HR	1
Cyperaceae	*Isolepis cernua* (Vahl) Roem. & Schult.	HR	1
Cyperaceae	*Isolepis habra* (Edgar) Soják	HR	4
Cyperaceae	*Isolepis marginata* (Thunb.) A.Dietr.**	HR	4
Junglandaceae	*Juglans regia* L.**	TR	2

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Family	Species	Growth forms	Sp.occurence
Juncaceae	*Juncus articulatus* L.**	HR	15
Juncaceae	*Juncus australis* Hook.f.	HR	16
Juncaceae	*Juncus bufonius* L.**	HR	38
Juncaceae	*Juncus distegus* Edgar	HR	190
Juncaceae	*Juncus edgariae* L.A.S.Johnson & K.L.Wilson	HR	60
Juncaceae	*Juncus effusus* L.**	HR	6
Juncaceae	*Juncus filicaulis* Buchenau**	HR	5
Juncaceae	*Juncus kraussii* Hochst.	HR	1
Juncaceae	*Juncus novae-zelandiae* Hook.f.	HR	1
Juncaceae	*Juncus planifolius* R.Br.	HR	3
Juncaceae	*Juncus sarophorus* L.A.S.Johnson	HR	2
Juncaceae	*Juncus* spp. L.	HR	1
Juncaceae	*Juncus tenuis* Willd.**	HR	4
Poaceae	*Koeleria novozelandica* Domin	GR	1
Myrtaceae	*Kunzea ericoides* (A.Rich.) Joy Thomps.	TR	103
Poaceae	*Lachnagrostis pilosa* (Buchanan) Edgar	GR	2
Poaceae	*Lachnagrostis* spp. Trin.	GR	3
Asteraceae	*Lactuca serriola* L.**	HR	2
Asteraceae	*Lagenifera cuneata* Petrie	HR	1
Asteraceae	*Lagenifera pinnatifida* Hook.f.	HR	4
Asteraceae	*Lagenifera pumila* (G.Forst.) Cheeseman	HR	13
Asteraceae	*Lagenifera strangulata* Colenso	HR	15

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Family	Species	Growth forms	Sp.occurence
Poaceae	*Lagurus ovatus* L.**	GR	2
Lamiaceae	*Lamium purpureum* L.**	HR	1
Aizoaceae	*Lampranthus* spp. N.E.Br.**	HR	1
Dryopteridaceae	*Lastreopsis hispida* (Sw.) Tindale	FE	1
Dryopteridaceae	*Lastreopsis velutina* (A.Rich.) Tindale	FE	1
Asteraceae	*Leontodon saxatilis* Lamarck**	HR	117
Brassicaceae	*Lepidium africanum* (Burm.f.) DC.**	HR	2
Brassicaceae	*Lepidium desvauxii* Thell.**	HR	5
Brassicaceae	*Lepidium didymum* L.**	HR	1
Brassicaceae	*Lepidium draba* L.**	HR	1
Brassicaceae	*Lepidium hyssopifolium* Desv.**	HR	1
Brassicaceae	*Lepidium pseudotasmanicum* Thell.**	HR	6
Brassicaceae	*Lepidium* spp. L.**	HR	1
Brassicaceae	*Lepidium squamatum* Forssk.**	HR	4
Ericaceae	*Leptecophylla juniperina* (J.R.Forst. & G.Forst.) C.M.Weiller	SH	1
Asteraceae	*Leptinella dioica* Hook.f.	HR	54
Asteraceae	*Leptinella minor* Hook.f.	HR	18
Asteraceae	*Leptinella pusilla* Hook.f.	HR	4
Asteraceae	*Leptinella squalida* Hook.f.	HR	4
Osmundaceae	*Leptopteris hymenophylloides* (A.Rich.) C.Presl	FE	4
Myrtaceae	*Leptospermum scoparium* J.R.Forst. & G.Forst.	SH	1
Rubiaceae	*Leptostigma setulosa* (Hook.f.) Fosberg	HR	8

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Family	Species	Growth forms	Sp.occurence
Asteraceae	*Leucanthemum vulgare* Lam.**	HR	1
Ericaceae	*Leucopogon fasciculatus* (G.Forst.) A.Rich.	SH	1
Ericaceae	*Leucopogon fraseri* A.Cunn.	SH	23
Caprifoliaceae	*Leycesteria formosa* Wall.**	SH	1
Iridaceae	*Libertia ixioides* (G.Forst.) Spreng.	HR	8
Apiaceae	*Lilaeopsis novae-zelandiae* (Gand.) A.W.Hill	HR	1
Ericaceae	*Linaria purpurea* (L.) Mill.**	HR	1
Linaceae	*Linum bienne* Mill.**	HR	49
Linaceae	*Linum catharticum* L.**	HR	7
Linaceae	*Linum monogynum* G.Forst.	HR	4
Campanulaceae	*Lobelia angulata* G.Forst.	HR	1
Brassicaceae	*Lobularia maritima* (L.) Desv.**	HR	1
Poaceae	*Lolium multiflorum* Lam.**	GR	7
Poaceae	*Lolium perenne* L.**	GR	940
Myrtaceae	*Lophomyrtus bullata* (Sol. ex A.Cunn.) Burret	SH	1
Myrtaceae	*Lophomyrtus obcordata* (Raoul) Burret	TR	20
Fabaceae	*Lotus pedunculatus* Cav.**	HR	1
Juncaceae	*Luzula banksiana* var. *orina* Edgar	HR	12
Juncaceae	*Luzula congesta* (Thuill.) Lej.**	HR	1
Juncaceae	*Luzula picta* A.Rich.	HR	1
Juncaceae	*Luzula picta* var. limosa Edgar	HR	1
Juncaceae	*Luzula picta* var. *pallida* (Hook.f.) Edgar	HR	1

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Family	Species	Growth forms	Sp.occurence
Juncaceae	*Luzula rufa* Edgar	HR	23
Solanaceae	*Lycium ferocissimum* Miers**	SH	4
Lycopodiaceae	*Lycopodium fastigiatum* R.Br.	FE	1
Lythraceae	*Lythrum hyssopifolia* L.**	HR	1
Piperaceae	*Macropiper excelsum* (G.Forst.) Miq.	SH	41
Rosaceae	*Malus* ×*domestica* Borkh.**	TR	3
Malvaceae	*Malva arborea* L.**	HR	1
Malvaceae	*Malva linnaei* M.F.Ray**	HR	3
Malvaceae	*Malva neglecta* Wallr.**	HR	10
Malvaceae	*Malva nicaeensis* All.**	HR	4
Malvaceae	*Malva sylvestris* L.**	HR	1
Lamiaceae	*Marrubium vulgare* L.**	HR	20
Asteraceae	*Matricaria discoidea* DC.**	HR	2
Fabaceae	*Medicago arabica* (L.) Huds.**	HR	11
Fabaceae	*Medicago lupulina* L.**	HR	8
Fabaceae	*Medicago nigra* (L.) Krock.**	HR	10
Fabaceae	*Medicago sativa* L.**	HR	4
Fabaceae	*Medicago* spp. L.**	HR	1
Rutaceae	*Melicope simplex* A.Cunn.	SH	33
Violaceae	*Melicytus alpinus* (Kirk) Garn.-Jones	SH	15
Violaceae	*Melicytus crassifolius* (Hook.f.) Garn.-Jones	SH	39
Violaceae	*Melicytus ramiflorus* J.R.Forst. & G.Forst.	TR	157

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Family	Species	Growth forms	Sp.occurence
Violaceae	*Melicytus* spp. J.R.Forst. & G.Forst.	SH	1
Fabaceae	*Melilotus indicus* (L.) All.**	HR	1
Lamiaceae	*Mentha cunninghamii* Benth.	HR	7
Myrtaceae	*Metrosideros diffusa* (G.Forst.) Sm.	TR	5
Poaceae	*Microlaena avenacea* (Raoul) Hook.f.	GR	2
Poaceae	*Microlaena polynoda* (Hook.f.) Hook.f.	GR	4
Poaceae	*Microlaena stipoides* (Labill.) R.Br.	GR	68
Polypodiaceae	*Microsorum pustulatum* (G.Forst.) Copel.	FE	26
Orchidaceae	*Microtis oligantha* L.B.Moore	HR	4
Orchidaceae	*Microtis unifolia* (G.Forst.) Rchb.f.	HR	110
Ericaceae	*Mimulus guttatus* DC.**	HR	14
Ericaceae	*Mimulus moschatus* Lindl.**	HR	12
Ericaceae	*Mimulus repens* R.Br.	HR	1
Portulacaceae	*Montia fontana* L.	HR	7
Polygonaceae	*Muehlenbeckia australis* (G.Forst.) Meisn.	SH	181
Polygonaceae	*Muehlenbeckia complexa* (A.Cunn.) Meisn.	SH	208
Asteraceae	*Mycelis muralis* (L.) Dumort.**	HR	40
Myoporaceae	*Myoporum laetum* G.Forst.	TR	13
Boraginaceae	*Myosotis arvensis* (L.) Hill**	HR	1
Boraginaceae	*Myosotis laxa* subsp. *caespitosa* (Schultz) Hyl. ex Nordh.**	HR	2
Boraginaceae	*Myosotis spathulata* G.Forst.	HR	1
Myrsinaceae	*Myrsine australis* (A.Rich.) Allan	TR	44

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Family	Species	Growth forms	Sp.occurence
Myrsinaceae	*Myrsine divaricata* A.Cunn.	SH	18
Brassicaceae	*Nasturtium microphyllum* Boenn. ex Rchb.**	HR	12
Brassicaceae	*Nasturtium officinale* R.Br.**	HR	1
Orchidaceae	*Nematoceras macranthum* Hook.f.	HR	1
Orchidaceae	*Nematoceras trilobum* Hook.f.	HR	5
Myrtaceae	*Neomyrtus pedunculata* (Hook.f.) Allan	SH	2
Rubiaceae	*Nertera depressa* Banks & Sol. ex Gaertn.	HR	2
Nothofagaceae	*Nothofagus fusca* (Hook.f.) Oerst. (1873)	TR	1
Asteraceae	*Olearia ilicifolia* Hook.f.	SH	4
Asteraceae	*Olearia paniculata* (J.R.Forst. & G.Forst.) Druce	TR	7
Ophioglossaceae	*Ophioglossum coriaceum* A.Cunn.	FE	31
Orobanchaceae	*Orobanche minor* Sm.**	HR	20
Ericaceae	*Ourisia macrophylla* subsp. *lactea* (L.B.Moore) Meudt	HR	2
Oxalidaceae	*Oxalis articulata* Savigny**	HR	3
Oxalidaceae	*Oxalis corniculata* L.**	HR	18
Oxalidaceae	*Oxalis exilis* A.Cunn.	HR	292
Oxalidaceae	*Oxalis latifolia* Kunth**	HR	1
Oxalidaceae	*Oxalis rubens* Haw.	HR	27
Dennstaedtiaceae	*Paesia scaberula* (A.Rich.) Kuhn	FE	2
Poaceae	*Parapholis incurva* (L.) C.E.Hubb.**	GR	1
Ericaceae	*Parentucellia viscosa* (L.) Caruel**	HR	9
Urticaceae	*Parietaria debilis* G.Forst.	HR	4

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Family	Species	Growth forms	Sp.occurence
Apocynaceae	*Parsonsia capsularis* (G.Forst.) R.Br.	SH	20
Apocynaceae	*Parsonsia heterophylla* A.Cunn.	SH	94
Poaceae	*Paspalum dilatatum* Poir.**	GR	1
Passifloraceae	*Passiflora tetrandra* Banks ex DC.	SH	4
Apiaceae	*Pastinaca sativa* L.**	HR	1
Geraniaceae	*Pelargonium inodorum* Willd.	HR	6
Pteridaceae	*Pellaea calidirupium* Brownsey & Lovis	FE	1
Pteridaceae	*Pellaea rotundifolia* (G.Forst.) Hook.	FE	61
Pennantiaceae	*Pennantia corymbosa* J.R.Forst. & G.Forst.	TR	73
Polygonaceae	*Persicaria maculosa* Gray**	HR	4
Apiaceae	*Petroselinum crispum* (Mill.) A.W.Hill**	HR	4
Poaceae	*Phalaris minor* Retz.**	GR	3
Poaceae	*Phleum pratense* L.**	GR	65
Phormiaceae	*Phormium cookianum* Le Jol.	GR	4
Phormiaceae	*Phormium tenax* J.R.Forst. & G.Forst.	GR	8
Phytolaccaceae	*Phytolacca octandra* L.**	HR	1
Asteraceae	*Pilosella officinarum* Vaill.**	HR	1
Pinaceae	*Pinus radiata* D.Don**	TR	13
Pittosporaceae	*Pittosporum eugenioides* A.Cunn.	TR	26
Pittosporaceae	*Pittosporum tenuifolium* Sol. ex Gaertn.	TR	39
Malvaceae	*Plagianthus divaricatus* J.R.Forst. & G.Forst.	SH	1
Malvaceae	*Plagianthus regius* (Poit.) Hochr.	TR	34

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Family	Species	Growth forms	Sp.occurence
Malvaceae	*Plagianthus regius* (Poit.) Hochr. subsp. *regius*	TR	1
Plantaginaceae	*Plantago coronopus* L.**	HR	10
Plantaginaceae	*Plantago lanceolata* L.**	HR	341
Plantaginaceae	*Plantago major* L.**	HR	14
Plantaginaceae	*Plantago raoulii* Decne.	HR	2
Thelypteridaceae	*Pneumatopteris pennigera* (G.Forst.) Holttum	FE	12
Poaceae	*Poa anceps* G.Forst.	GR	9
Poaceae	*Poa annua* L.**	GR	80
Poaceae	*Poa cita* Edgar	GR	352
Poaceae	*Poa colensoi* Hook.f.	GR	2
Poaceae	*Poa imbecilla* Spreng.	GR	10
Poaceae	*Poa infirma* Kunth**	GR	4
Poaceae	*Poa matthewsii* Petrie	GR	44
Poaceae	*Poa pratensis* L.**	GR	380
Poaceae	*Poa trivialis* L.**	GR	31
Podocarpaceae	*Podocarpus hallii* Kirk	TR	23
Podocarpaceae	*Podocarpus totara* G.Benn. ex D.Don	TR	12
Caryophyllaceae	*Polycarpon tetraphyllum* L.**	HR	93
Polygonaceae	*Polygonum aviculare* L.**	HR	18
Dryopteridaceae	*Polystichum neozelandicum* Fée	FE	190
Dryopteridaceae	*Polystichum oculatum* (Hook.) J.B.Armstr.	FE	1
Dryopteridaceae	*Polystichum vestitum* (G.Forst.) C.Presl	FE	113

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Family	Species	Growth forms	Sp.occurence
Orchidaceae	*Prasophyllum colensoi* Hook.f.	HR	11
Podocarpaceae	*Prumnopitys taxifolia* (D.Don) de Laub.	HR	8
Lamiaceae	*Prunella vulgaris* L.**	HR	51
Rosaceae	*Prunus cerasifera* Ehrh.**	TR	7
Asteraceae	*Pseudognaphalium luteoalbum* (L.) Hilliard & B.L.Burtt	HR	12
Araliaceae	*Pseudopanax arboreus* (Murray) Philipson	TR	55
Araliaceae	*Pseudopanax colensoi* (Hook.f.) Philipson	TR	18
Araliaceae	*Pseudopanax crassifolius* (Sol. ex A.Cunn.) K.Koch	TR	25
Araliaceae	*Pseudopanax ferox* Kirk	TR	5
Pinaceae	*Pseudotsuga menziesii* (Mirb.) Franco**	TR	1
Winteraceae	*Pseudowintera colorata* (Raoul) Dandy	TR	46
Dennstaedtiaceae	*Pteridium esculentum* (G.Forst.) Cockayne	FE	169
Pteridaceae	*Pteris tremula* R.Br.	FE	1
Orchidaceae	*Pterostylis areolata* Petrie	HR	17
Orchidaceae	*Pterostylis australis* Hook.f.	HR	6
Orchidaceae	*Pterostylis graminea* Hook.f.	HR	17
Orchidaceae	*Pterostylis montana* Hatch	HR	4
Orchidaceae	*Pterostylis* spp. R.Br.	HR	2
Poaceae	*Puccinellia* spp. Parl.	GR	3
Poaceae	*Puccinellia stricta* (Hook.f.) C.H.Blom	GR	1
Poaceae	*Puccinellia walkeri* (Kirk) Allan	GR	1
Fagaceae	*Quercus robur* L.**	TR	1

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Family	Species	Growth forms	Sp.occurence
Ranunculaceae	*Ranunculus foliosus* Kirk	HR	8
Ranunculaceae	*Ranunculus glabrifolius* Hook.	HR	7
Ranunculaceae	*Ranunculus multiscapus* Hook.f.	HR	3
Ranunculaceae	*Ranunculus parviflorus* L.**	HR	21
Ranunculaceae	*Ranunculus reflexus* Garn.-Jones	HR	57
Ranunculaceae	*Ranunculus repens* L.**	HR	38
Ranunculaceae	*Ranunculus sardous* Crantz**	HR	1
Ranunculaceae	*Ranunculus sceleratus* L.**	HR	3
Asteraceae	*Raoulia glabra* Hook.f.	HR	12
Asteraceae	*Raoulia subsericea* Hook.f.	HR	4
Araliaceae	*Raukaua anomalus* (Hook.) A.D.Mitch., Frodin & Heads	TR	1
Grossulariaceae	*Ribes sanguineum* Pursh**	SH	3
Grossulariaceae	*Ribes uva-crispa* L.**	SH	1
Ripogonaceae	*Ripogonum scandens* J.R.Forst. & G.Forst.	SH	29
Iridaceae	*Romulea minutiflora* Klatt**	HR	1
Rosaceae	*Rosa rubiginosa* L.**	SH	15
Rosaceae	*Rubus caesius* L.**	SH	1
Rosaceae	*Rubus cissoides* A.Cunn.	SH	62
Rosaceae	*Rubus fruticosus* L.**	SH	12
Rosaceae	*Rubus idaeus* L.**	SH	1
Rosaceae	*Rubus schmidelioides* A.Cunn.	SH	21
Rosaceae	*Rubus schmidelioides* var. *subpauperatus* (Cockayne) Allan	SH	5

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Family	Species	Growth forms	Sp.occurence
Rosaceae	*Rubus squarrosus* Fritsch	SH	3
Polygonaceae	*Rumex acetosella* L.**	HR	360
Polygonaceae	*Rumex crispus* L.**	HR	32
Polygonaceae	*Rumex flexuosus* Sol. ex G.Forst.	HR	6
Polygonaceae	*Rumex obtusifolius* L.**	HR	42
Polygonaceae	*Rumex pulcher* L.**	HR	29
Poaceae	*Rytidosperma buchananii* (Hook.f.) Connor & Edgar	GR	1
Poaceae	*Rytidosperma caespitosum* (Gaudich.) Connor & Edgar**	GR	56
Poaceae	*Rytidosperma clavatum* (Zotov) Connor & Edgar	GR	430
Poaceae	*Rytidosperma corinum* Connor & Edgar	GR	2
Poaceae	*Rytidosperma gracile* (Hook.f.) Connor & Edgar	GR	59
Poaceae	*Rytidosperma merum* Connor & Edgar	GR	8
Poaceae	*Rytidosperma pilosum* (R.Br.) Connor & Edgar**	GR	2
Poaceae	*Rytidosperma racemosum* (R.Br.) Connor & Edgar**	GR	164
Poaceae	*Rytidosperma* spp. Steud.	GR	6
Poaceae	*Rytidosperma thomsonii* (Buchanan) Connor & Edgar	GR	12
Poaceae	*Rytidosperma unarede* (Raoul) Connor & Edgar	GR	94
Caryophyllaceae	*Sagina apetala* Ard.**	HR	49
Caryophyllaceae	*Sagina procumbens* L.**	HR	166
Salicaceae	*Salix* ×*fragilis* L.**	TR	3
Salicaceae	*Salix cinerea* L.**	TR	1
Caprifoliaceae	*Sambucus nigra* L.**	TR	31

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Family	Species	Growth forms	Sp.occurence
Amaranthaceae	*Sarcocornia quinqueflora* (Bunge ex Ung.-Sternb.) A.J.Scott subsp. *quinqueflora*	HR	4
Apiaceae	*Scandia geniculata* (G.Forst.) J.W.Dawson	HR	29
Poaceae	*Schedonorus arundinaceus* (Schreb.) Dumort.**	GR	15
Araliaceae	*Schefflera digitata* J.R.Forst. & G.Forst.	TR	35
Apiaceae	*Schizeilema trifoliolatum* (Hook.f.) Domin	HR	14
Cyperaceae	*Schoenoplectus pungens* (Vahl) Palla	HR	1
Caryophyllaceae	*Scleranthus brockiei* P.A.Williamson	HR	3
Caryophyllaceae	*Scleranthus uniflorus* P.A.Williamson	HR	1
Poaceae	*Secale cereale* L.**	GR	1
Crassulaceae	*Sedum acre* L.**	HR	1
Crassulaceae	*Sedum praealtum* A.DC.**	HR	1
Goodeniaceae	*Selliera radicans* Cav.	HR	1
Asteraceae	*Senecio carnosulus* (Kirk) C.J.Webb	HR	1
Asteraceae	*Senecio glaucophyllus* Cheeseman	HR	1
Asteraceae	*Senecio glaucophyllus* subsp. *basinudus* Ornduff	HR	8
Asteraceae	*Senecio glomeratus* Poir.	HR	23
Asteraceae	*Senecio jacobaea* L.**	HR	3
Asteraceae	*Senecio lautus* G.Forst. ex Willd.	HR	1
Asteraceae	*Senecio minimus* Poir.	HR	29
Asteraceae	*Senecio quadridentatus* Labill.	HR	7
Asteraceae	*Senecio sylvaticus* L.**	HR	1
Asteraceae	*Senecio vulgaris* L.**	HR	3

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Family	Species	Growth forms	Sp.occurence
Asteraceae	*Senecio wairauensis* Belcher	HR	3
Rubiaceae	*Sherardia arvensis* L.**	HR	48
Caryophyllaceae	*Silene coronaria* (L.) Clairv.**	HR	1
Caryophyllaceae	*Silene gallica* L.**	HR	168
Asteraceae	*Silybum marianum* (L.) Gaertn.**	HR	44
Brassicaceae	*Sisymbrium officinale* (L.) Scop.**	HR	89
Brassicaceae	*Sisymbrium orientale* L.**	HR	2
Solanaceae	*Solanum aviculare* G.Forst. var. *aviculare*	SH	3
Solanaceae	*Solanum chenopodioides* Lam.**	HR	2
Solanaceae	*Solanum dulcamara* L.**	HR	2
Solanaceae	*Solanum laciniatum* Aiton	SH	4
Solanaceae	*Solanum marginatum* L.f.**	SH	1
Solanaceae	*Solanum nigrum* L.**	HR	22
Asteraceae	*Solenogyne dominii* L.G.Adams**	HR	3
Asteraceae	*Solenogyne gunnii* (Hook.f.) Cabrera**	HR	4
Asteraceae	*Solenogyne* spp. Cass.**	HR	1
Asteraceae	*Sonchus asper* (L.) Hill**	HR	27
Asteraceae	*Sonchus oleraceus* L.**	HR	83
Fabaceae	*Sophora microphylla* Aiton	TR	59
Fabaceae	*Sophora prostrata* Buchanan	SH	6
Caryophyllaceae	*Spergula arvensis* L.**	HR	4
Caryophyllaceae	*Spergularia marina* (L.) Griseb.**	HR	2

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Family	Species	Growth forms	Sp.occurence
Caryophyllaceae	*Spergularia rubra* (L.) J.Presl & C.Presl**	HR	6
Caryophyllaceae	*Spergularia tasmanica* (Kindb.) L.G.Adams	HR	1
Poaceae	*Sporobolus africanus* (Poir.) A.Robyns & Tournay**	GR	1
Lamiaceae	*Stachys arvensis* (L.) L.**	HR	1
Stackhousiaceae	*Stackhousia minima* Hook.f.	HR	1
Caryophyllaceae	*Stellaria alsine* Grimm**	HR	6
Caryophyllaceae	*Stellaria decipiens* Hook.f.	HR	37
Caryophyllaceae	*Stellaria gracilenta* Hook.f.	HR	1
Caryophyllaceae	*Stellaria media* (L.) Vill.**	HR	209
Caryophyllaceae	*Stellaria parviflora* Hook.f.	HR	29
Moraceae	*Streblus heterophyllus* (Blume) Corner	TR	8
Asteraceae	*Stuartina muelleri* Sond.**	HR	4
Asteraceae	*Taraxacum officinale* F.H.Wigg.**	HR	313
Orchidaceae	*Thelymitra hatchii* L.B.Moore	HR	6
Orchidaceae	*Thelymitra longifolia* J.R.Forst. & G.Forst.	HR	16
Psilotaceae	*Tmesipteris elongata* P.A.Dang.	FE	1
Psilotaceae	*Tmesipteris tannensis* (Spreng.) Bernh.	FE	1
Apiaceae	*Torilis nodosa* (L.) Gaertn.**	HR	23
Arecaceae	*Trachycarpus fortunei* (Hook.) H.Wendl.**	TR	1
Asteraceae	*Tragopogon porrifolius* L.**	HR	1
Hymenophyllaceae	*Trichomanes venosum* R.Br.	FE	4
Fabaceae	*Trifolium arvense* L.**	HR	5

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Family	Species	Growth forms	Sp.occurence
Fabaceae	*Trifolium campestre* Schreb.**	HR	8
Fabaceae	*Trifolium dubium* Sibth.**	HR	672
Fabaceae	*Trifolium fragiferum* L.**	HR	10
Fabaceae	*Trifolium glomeratum* L.**	HR	287
Fabaceae	*Trifolium micranthum* Viv.**	HR	16
Fabaceae	*Trifolium ornithopodioides* L.**	HR	3
Fabaceae	*Trifolium pratense* L.**	HR	115
Fabaceae	*Trifolium repens* L.**	HR	947
Fabaceae	*Trifolium* spp. L.**	HR	2
Fabaceae	*Trifolium striatum* L.**	HR	249
Fabaceae	*Trifolium subterraneum* L.**	HR	229
Fabaceae	*Trifolium suffocatum* L.**	HR	1
Fabaceae	*Trifolium tomentosum* L.**	HR	3
Asteraceae	*Tripleurospermum inodorum* Sch.Bip.**	HR	4
Poaceae	*Trisetum lepidum* Edgar & A.P.Druce	GR	1
Poaceae	*Triticum aestivum* L.**	GR	1
Poaceae	*Triticum* spp. L.**	GR	1
Loranthaceae	*Tupeia antarctica* (G.Forst.) Cham. & Schltdl.	TR	2
Fabaceae	*Ulex europaeus* L.**	SH	94
Cyperaceae	*Uncinia leptostachya* Raoul	HR	9
Cyperaceae	*Uncinia rubra* Boott	HR	26
Cyperaceae	*Uncinia rupestris* Raoul	HR	3

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Family	Species	Growth forms	Sp.occurence
Cyperaceae	*Uncinia scabra* Boott	HR	2
Cyperaceae	*Uncinia* spp. Pers.	HR	1
Cyperaceae	*Uncinia uncinata* (L.f.) K′uk.	HR	16
Urticaceae	*Urtica ferox* G.Forst.	HR	105
Urticaceae	*Urtica incisa* Poir.	HR	4
Urticaceae	*Urtica urens* L.**	HR	10
Ericaceae	*Verbascum thapsus* L.**	HR	63
Ericaceae	*Verbascum virgatum* Stokes**	HR	1
Verbenaceae	*Verbena officinalis* L.**	HR	1
Ericaceae	*Veronica arvensis* L.**	HR	126
Ericaceae	*Veronica persica* Poir.**	HR	5
Ericaceae	*Veronica serpyllifolia* L.**	HR	1
Fabaceae	*Vicia hirsuta* (L.) Gray**	HR	32
Fabaceae	*Vicia lutea* L.**	HR	3
Fabaceae	*Vicia sativa* L.**	HR	545
Fabaceae	*Vicia tetrasperma* (L.) Schreb.**	HR	5
Apocynaceae	*Vinca major* L.**	HR	1
Violaceae	*Viola cunninghamii* Hook.f.	HR	55
Violaceae	*Viola filicaulis* Hook.f.	HR	3
Asteraceae	*Vittadinia australis* A.Rich.	HR	6
Asteraceae	*Vittadinia gracilis* (Hook.f.) N.T.Burb.**	HR	28
Poaceae	*Vulpia bromoides* (L.) Gray**	GR	338

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Family	Species	Growth forms	Sp.occurence
Poaceae	*Vulpia myuros* (L.) C.C.Gmel. var. *myuros***	GR	9
Campanulaceae	*Wahlenbergia albomarginata* Hook.	HR	3
Campanulaceae	*Wahlenbergia gracilis* (G.Forst.) A.DC.	HR	258

Appendix R

GIS model Banks Peninsula geodatabase

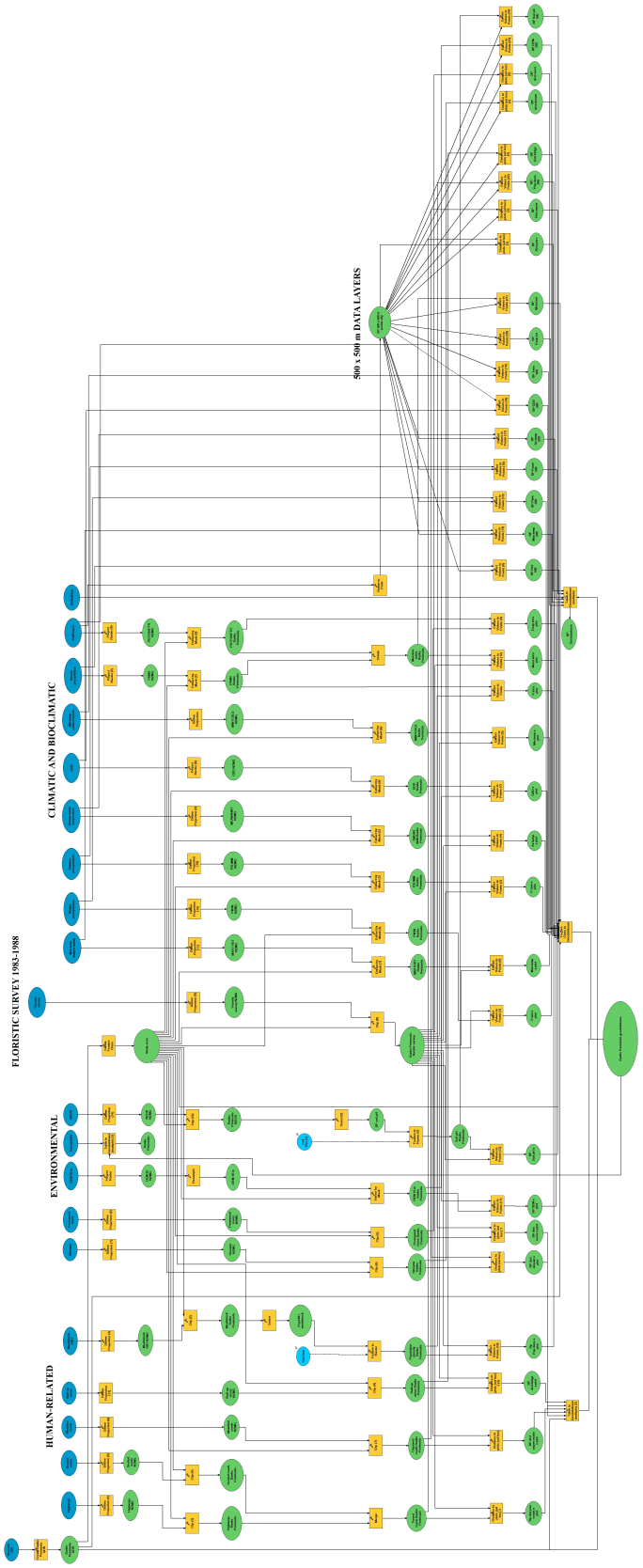

Figure R.1. A3 paper size of the GIS model from the Banks Peninsula geodatabase using ModelBuilder application in ArcGIS 9.3. Blue = input data; yellow = GIS tools; green = output data.

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